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Optimized Plankton Ecosystem Dynamics Model

Progress in Development for Predicting Ocean Light Transmission

Titan Systems, Inc.

NAVAL OCEAN SYSTEMS CENTER

San Diego, California 92152-5000

E. G. SCHWEIZER, CAPT, USN
Commander

R. M. HILLYER
Technical Director

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The Optimized Plankton Ecosystem Dynamics (OPED) Model computes the interactive rate processes and resulting vertical distributions of planktonic and chemical constituents within the ocean water column. Inherent in the model formulation are optical properties which dictate the light field and, hence, the photosynthetic response of the phytoplankton within the water column. The current version of OPED can be used to analyze available oceanographic data and to establish appropriate "tuned" parameters representative of the associated oceanographic province. Optical properties as well as plankton and chemical concentrations can then be predicted in time or space as a function of the fundamental physical driving forces including solar insolation and wind mixing.

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1. INTRODUCTION

The Optimized Plankton Ecosystem Dynamics (OPED) Model computes the interactive rate processes and resulting vertical distributions of planktonic and chemical constituents within the ocean water column. Inherent in the model formulation are optical properties which dictate the light field and, hence, the photosynthetic response of the phytoplankton within the water column. The current version of OPED can be used to analyze available oceanographic data and to establish appropriate "tuned" parameters representative of the associated oceanographic province. Optical properties as well as plankton and chemical concentrations can then be predicted in time or space as a function of the fundamental physical driving forces including solar insolation and wind mixing.

The focus of the present study has been to improve the OPED Model formulation based on detailed studies of Weather Stations P and S. This development builds on the previous OPED modeling work by Atkinson (1987a) and is based on the general ecosystem analysis approach described in Atkinson (1987b).

2. OPED MODEL OVERVIEW

A general description of the OPED Model is given below, while details of the improvements made during this past year are presented in the following section.

2.1 Model Equations

The OPED Model consists of a coupled set of dynamics equations that describes the diffusion and biochemical interactions of four primary ecosystem constituents: dissolved nutrients, phytoplankton, zooplankton, and predators. For the passive (non-swimming) components (i.e., dissolved nutrients, phytoplankton), the governing equations are of the form:

$$\frac{\partial C}{\partial t} - \frac{\partial}{\partial z}\left(K \frac{\partial C}{\partial z}\right) + W \frac{\partial C}{\partial z} = \dot{C} \qquad (1)$$

where C is the constituent concentration, K is the vertical turbulent diffusion coefficient, w is the net vertical velocity (sinking or upwelling as appropriate), and $\dot{C}$ is the net production due to biochemical interactions.

For active migrators (i.e., zooplankton, predators), the diffusion and sinking terms in Equation 1 are deleted and a vertical distribution function is used to establish the concentrations within each depth layer. These distributions are assumed to represent daily time-averaged orientations of the active zooplankton and predator components who migrate over a diurnal cycle within the water column independent of diffusion processes. There are two optional distribution functions that can be selected in the current OPED Program version to describe this vertical orientation: (1) fractions of the total population within each depth strata, and (2) a gamma distribution defined by shape parameters (see Hoel *et al*, 1971).

The ecosystem constituents, whether active or passive, are coupled through the interactive rate term $\dot{C}$ in Equation 1. The schematic diagram in Figure 1 depicts the ecosystem where a visual predator has been added to the previous three component system (see Section 3.1). The flux of the tracer element nitrogen is shown with the interactions defined as follows:

$$\begin{aligned}
\dot{N} &= -(f_1-f_3)P + f_4\,Z + f_7\,V \\
\dot{P} &= (f_1-f_3)P - f_2\,Z \\
\dot{Z} &= (f_2-f_4-f_5)Z - f_6\,V \\
\dot{V} &= (f_6-f_7-f_8)V
\end{aligned} \qquad (2)$$

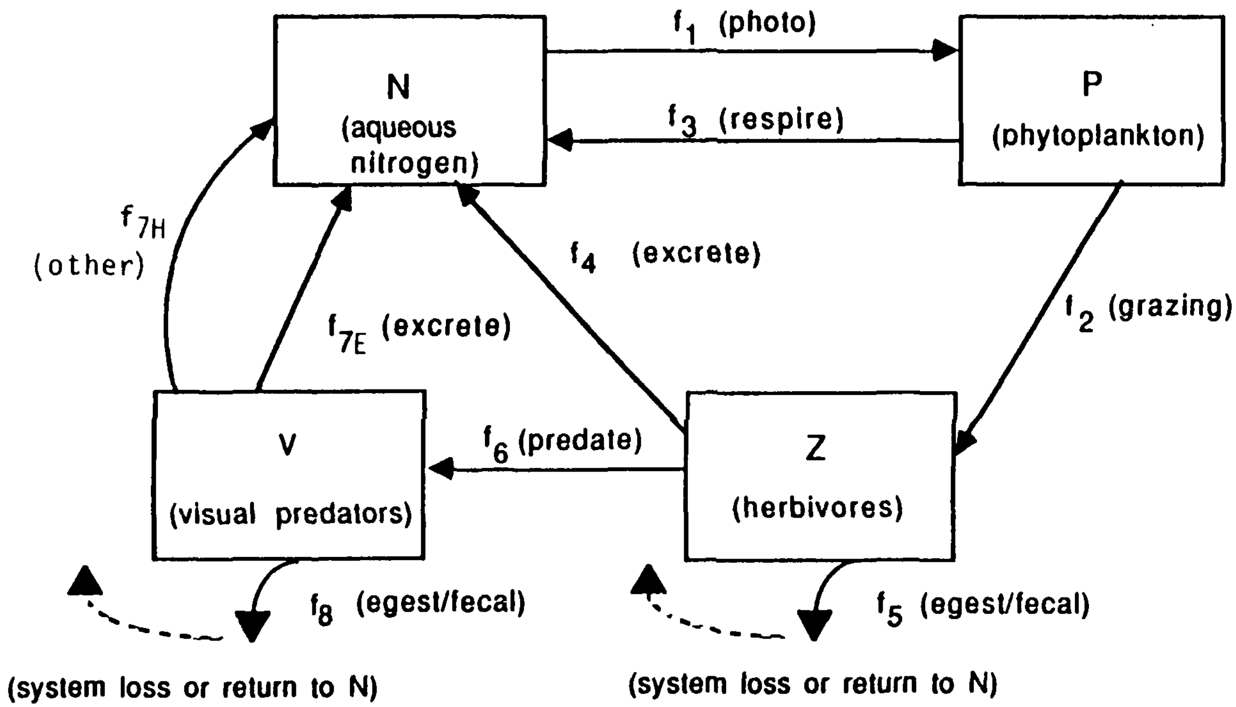


Figure 1. Conceptual OPED Model

In general, the specific rate terms, f_i, are functions of the concentrations and/or activity levels of the component from which the respective flux originates. The rate formulas are described in detail in Atkinson (1987a) while current study modifications are given in Section 3.1.

2.2 Solution Procedures

The OPED Model equations are formulated for numerical integration using second order forward difference approximations for the spatial derivatives and first order approximations for the temporal derivatives. The ocean is divided into a number of Δz vertical layers and time steps of Δt are defined.

The numerical formulation of the coupled set described by Equation 1 above can be solved either to determine steady state conditions ($\partial C/\partial t = 0$) or time varying responses. For the steady state case, an expanded capability allows for tuning of certain selected model parameters based on observed component concentration profiles and the underlying assumption of optimal solar energy utilization. The selected model parameters are treated as variables in formulating the problem as a nonlinear program. Constraint equations relate measured or assumed conditions within the vertical profiles and at the bottom boundary for any or all ecosystem components. An objective function defines the efficiency of solar energy utilization by the plankton and/or predators that is to be maximized.

A special nonlinear programming algorithm developed by Lasdon et al (1978) is used to solve the expanded steady-state problem. At each iteration in the optimal search procedure, the steady state equations are numerically integrated from the surface to the bottom boundary. It is these boundary conditions that must be matched to define realistic steady-state results. The NLP algorithm proceeds essentially as in a "shooting" procedure

(Hornbeck, 1975) to match constraints while searching for the maximum objective function value. Output includes the "tuned" model parameters consistent with the constraint relations and the optimization objective. This computational mode, referred to as the OPED/Optimization procedure, is described further by Atkinson (1987a, 1987b).

The second OPED computational mode performs the straightforward integration of the time varying equations based on initial component profiles and given model parameter values. The integration procedure steps down from the surface to the bottom boundary at each time point based on the conditions at the previous time point; no sophisticated iteration techniques are applied. This mode, called the OPED/Variational procedure, predicts dynamic response characteristics for the ecosystem acting under specified driving environmental forces including solar insolution, wind mixing, and deep ocean supplies of nutrients to the upper water column. The latter is specified by the nutrient concentration and gradient at the bottom boundary.

3. OPED MODEL IMPROVEMENTS

A number of significant modifcations have been incorporated in the OPED Model during the past year to improve both the ecosystem description and the numerical solution procedures. The improvements in the OPED Model are described below; this updated version has been used in the subsequent oceanographic data analysis presented in Sections 4 and 5.

3.1 Biochemical Descriptions

The major change to the biochemical formulas was the addition of a visual predator component to the ecosystem previously consisting of nutrients, phytoplankton, and zooplankton (herbivore). The visual predator component, which is quantified by its nitrogen

concentration as are the other components, feeds on the herbivore population (see Figure 1) with a rate that is dependent on ambient light levels. In this situation, the herbivore population has some advantage of predator avoidance in deeper, darker waters.

The governing equations for the new visual predator define the respective rate terms for predation, effective excretion, and egestion. The predation rate f_6 is given as a multiplicative saturation function of light level and prey concentration:

$$f_6 = g_E \cdot g_P \tag{3}$$

where

$$g_E = \begin{cases} a + \alpha E_z & , \quad 0 < E_{SAT} \\ b & , \quad E_z > E_{SAT} \end{cases} \tag{4}$$

and

$$g_P = \begin{cases} Z/Z_{SAT} & , \quad 0 < Z < Z_{SAT} \\ 1.0 & , \quad Z > Z_{SAT} \end{cases} \tag{5}$$

E_Z is defined as the average light level in the water column layer where the predator is feeding while E_{SAT} and Z_{SAT} are the saturation levels of light and prey concentration, respectively. The constants a, b, and E_{SAT} define the slope parameter α in Equation 4 :

$$\alpha = \frac{b-a}{E_{SAT}}$$

The effective excretion and egestion rates are:

$$f_7 = f_{7E} + f_{7H} \tag{6}$$
$$f_8 = c \cdot f_6 \tag{7}$$

The effective execretion is actually a composite term that describes constant predator nitrogen losses due to both excretion (f_{7E}) and higher tropic level predation or any other type loss (f_{7H}). The egestion rate is assumed proportional to the feeding rate.

In general, the above predator feeding relationships describe a visually orientated predator whose effectiveness increases with light level. The model parameters are ill defined from available literature data and can only be established based on the OPED/Optimization analysis described in Section 4. Future model developments can be used to upgrade the present formulas as available data warrants.

The other major change to the OPED biochemical formulas was the addition of a temperature dependent function for photosynthesis. While other models were considered (e.g., Frost 1987), the following Kiefer (1988a) semi-empirical development was selected as most applicable:

$$f_{1max} = \frac{f^{\infty}_{1max}}{1 + 3e^{-.18T}} \tag{8}$$

f_{1max} is the temperature dependent maximum photosynthetic rate; f^{∞}_{1max} is the ultimate or highest maximum rate; and T is the temperature in °C. Using f_{1max} as the maximum rate limit at the specified temperature, photosynthetic rate is further calculated as a function of the light or nutrient levels in a given water column layer according to the equations given by Atkinson (1987a).

3.2 Numerical Procedures

Two improvements were implemented in the OPED numerical solution procedures: (1) variable incremental layer depths (versus a single constant incremental depth), and (2) a computation iteration to determine consistent values for chlorophyll (CHl) and diffuse attenuation (k(PAR)) within any one layer. While the variable depth layer change is conceptually straightforward, it involved substantial programming changes throughout the OPED Program. The most significant change was to rederive the numerical integration formulas for the variable incremental depth case. The details of this derivation will not be presented here.

The values of CHl and k in a layer are implicitly related requiring an iterative procedure for solution. Each iteration cycle starts with a trial estimate and concludes with an error computation for diffuse attenuation k. The integrated form of the equation below defines the average chlorophyll level within a layer as a function of the assumed value for k. This chlorophyll level in turn defines a new k value based on a correlative formula given by Kiefer and Mitchell (1983).

$$\frac{CHl}{P} = \frac{f_1}{a^{*}\psi E_z} \qquad (9)$$

The parameter a* is a constant while the phytoplankton P are assumed known in the layer from the previous step in the numerical integration procedure. The following function is used for ψ :

$$\psi = \phi_m \frac{K_\phi}{K_\phi + E_z} \qquad (10)$$

where ϕ_m and K_ϕ are constants. The variations of f_1 (photosynthetic rate) and E_z (irradiance) within the layer are described by:

$$f_1 = \min \begin{cases} \dfrac{f_{1max}\, E_z}{K_E + E_z} \\[2ex] \dfrac{f_{1max}\, N}{K_N + N} \end{cases} \tag{11}$$

$$E_z = E_o\, e^{-kz} \tag{12}$$

where E_o is light level at the top of the layer, N is nitrogen concentration, and z is depth.

Equations 10, 11, and 12 are substituted into Equation 9 and integrated over the layer depth Δz for either light limiting or nutrient limiting phytoplankton growth. The integrated equations are:

Light Limiting Layer

$$\frac{CH1}{P} = \frac{f_{1max}}{a^* \phi_m K_\phi K_E k\Delta z} \cdot \left[k\Delta z\ (K_\phi + K_E) + K_\phi \ln\left(\frac{K_E + E_o e^{-k\Delta z}}{K_E + E_o}\right) + K_E \ln\left(\frac{K_E + E_o}{E_o + K_E e^{k\Delta z}}\right)\right] \tag{13}$$

Nutrient Limiting Layer

$$\frac{CHl}{P} = \frac{f_{1max}\ N\left[K_\phi(e^{k\Delta z}-1) + E_0 k\Delta z\right]}{a^*\ \phi_m K_\phi\ E_0 k\,\Delta z(K_N+N)} \qquad (14)$$

At each step in the iteration procedure, the CHl/value is computed for the estimated k value at that iteration. All other terms in Equations 13 and 14 are either constants or known variables for that layer. The next iterative value for k is then computed based on the Kiefer and Mitchell (1983) correlation:

$$k = C_1 + C_2 CHl + C_3 CHl^{2/3} \qquad (15)$$

where the constants C_1, C_2, and C_3 have been empirically derived from ocean data analyses. The procedure (Equations 13-15) is repeated for each new k estimate until a satisfactory k error between iterations is achieved. The process is very stable and converges rapidly to consistent CHl and k values within the layer.

3.3 Software Implementation

The OPED Program has been converted for use on a SUN 3/260 computer system enabling significant improvements in computational speed. In addition, the input/output formats have been expanded consistent with the updated models. A plotting capability has also been added for presenting simulation results; illustrations will be given in Sections 4 and 5.

4. OPED MODEL APPLICATION TO WEATHER STATION P ANALYSIS AND PREDICTION

The ecosystem dynamics at Station P are driven by the key physical oceanographic features illustrated in Figure 2. Solar irradiance and mixed layer depth are given for each month of the year based on data from the SUPER Program. These data are assumed to be typical of the yearly conditions, not only at Station P, but more generally within the central Gulf of Alaska subartic region. Further description of the yearly variation in thermo-structure at Station P is given by the monthly temperature profiles in Figure 3. The waters in this region are nutrient rich such that productivity is typically limited by the available light except right near the surface.

The initial objective in applying the OPED Model to Station P was to establish the general behavior and the practical limitations of the model for simulating observed conditions. An analysis was then conducted to estimate ("tune") the model parameter set for Station P. Predictions were made using the tuned model for comparison with representative data from this general oceanographic region.

4.1 General OPED Model Evaluation Studies

The fundamental modeling issues that were addressed during the initial Station P data studies were:

- selection of an appropriate objective function defining ecosystem energy efficiency which is to be maximized in the model tuning calculations.
- identification of critical ecosystem model parameters that "control" response characteristics and require special consideration in the model application

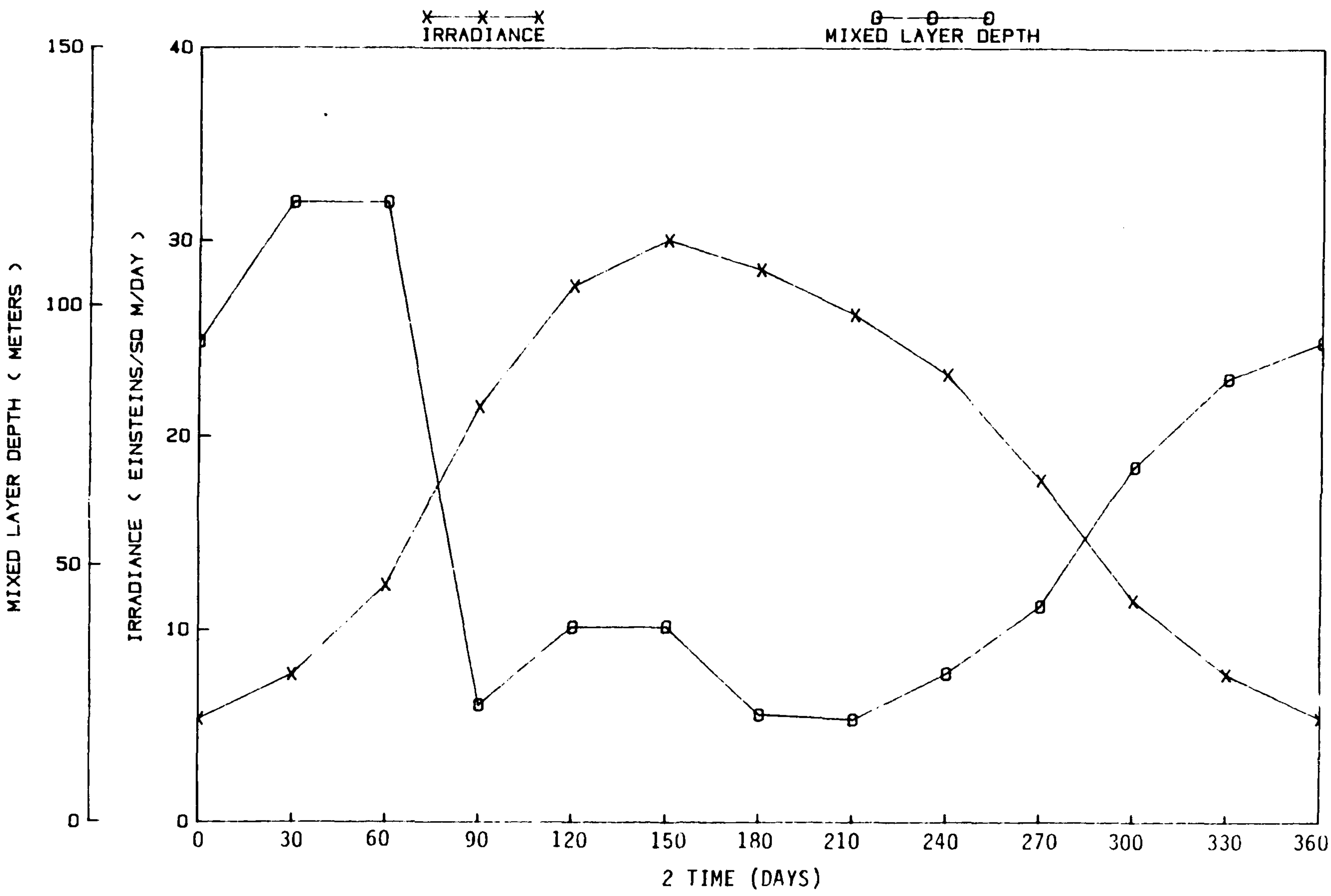


Figure 2. Variation of Surface Irradiance and Mixed Layer Depth over Year at Station P (from SUPER Program Data)

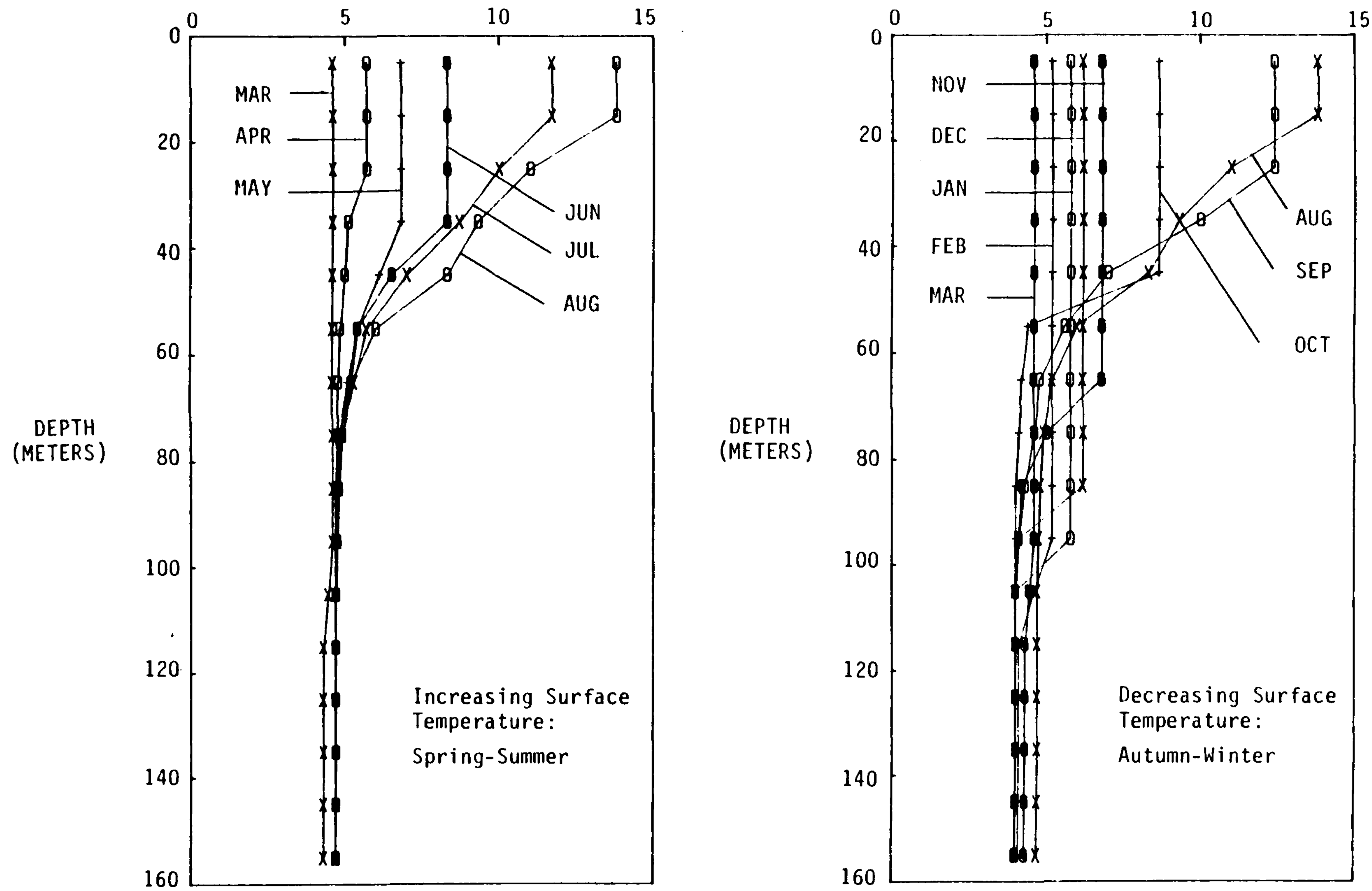


Figure 3. Monthly Temperature Profiles at Station P (from SUPER Program Data)

- stability of steady state solutions and correspondence of time step simulations to environmently-driven versus mathematically-induced responses

- necessity of the 4-component versus the 3-component ecosystem to describe vertical biochemical distributions

Objective Function. The optimization framework used for OPED Model tuning requires definitions of an objective function to be maximized (or minimized) in the solution procedure. The underlying assumption is that the oceanographic ecosystem will tend through evolutionary forces to make efficient use of the available solar energy resource that fuels biological production. One measure of this efficiency is the resultant percentage of the solar energy flux at the sea surface that is converted to net growth of phytoplankton, zooplankton and/or predator biomass.

After considering various alternatives, the selected objective function was the net growth efficiency of the highest trophic level: either the predator for the 4-component ecosystem or the zooplankton for the 3-component ecosystem. It was found that other lower trophic components must also produce efficiently in order to maximize the resultant food availability and growth potential for the highest trophic component. A series of test runs confirmed the reasonableness of this approach.

Critical Ecosystem Parameters. A range of values for OPED Model parameters were defined consistent with observations and understanding of the Station P ecosystem. The largest uncertainty involved the highest trophic level components, zooplankton and predators, whereas the photosynthetic response of phytoplankton is fairly well known from laboratory and field

investigations. A particularly significant factor was found to be the specific loss rate term which defines the effective nitrogen flux between the highest trophic level component and the aequeous nitrogen compartment. This rate corresponds to f7 in the 4-component model version shown in Figure 1 and encompasses not only the predator exectretion losses but also higher order predation and horizontal advective losses not explicitly accounted for in the modeling.

In order to bound the practical range for f7, a set of optimization runs were made with varying f7 values assumed. Steady state winter conditions at Station P (see next section) were used in the calculations. Both 3 and 4 component ecosystem formulations were run.

The results of the 4-component model calculations are given in Figure 4 where zooplankton and predator concentrations in the upper two 50 meter layers of the water column are plotted as a function of the f7 value. A sharp drop in the optimized predator concentrations is indicated as f7 increases from 0.01 to 0.1 per day. Concentration values greater than about 1 mg-at-N/m^3, which occur when f7 is less than about 0.05 per day, are considered to be unrealistic based on available Station P data. Zooplankton levels react less dramatically to the f7 increase. From these and similar results for the Station P optimization runs, a lower level of 0.05 per day was established with 0.10 per day as nominal. The nominal rate results in a surface zooplankton concentration of 0.15 mg-at-N/m^3 which is consistent with available data for Station P. For the 3-component calculations, analysis indicated similar specific loss rates were required to give reasonable concentration levels for the highest trophic component, zooplankton in this case.

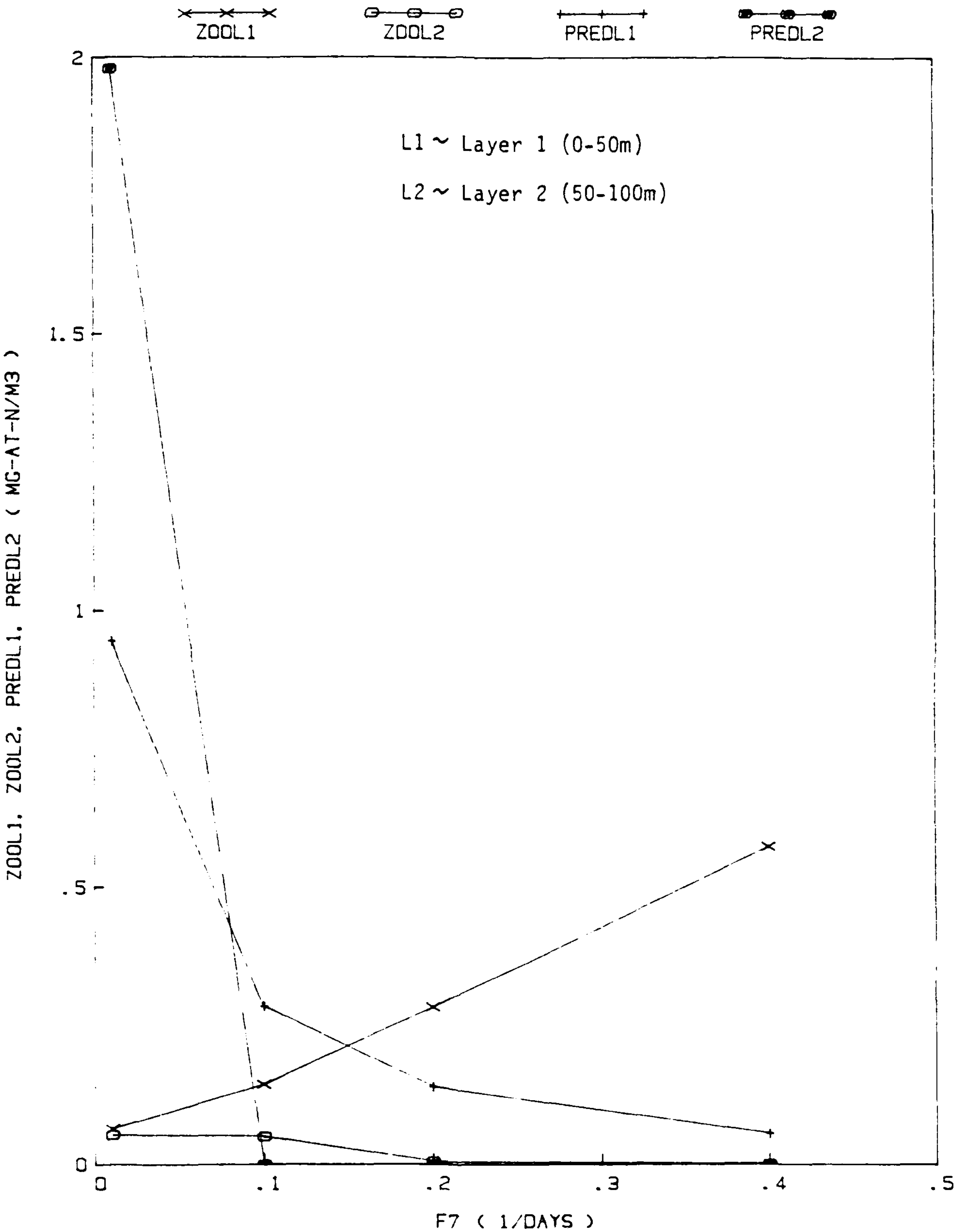


Figure 4. Optimal Zooplankton and Predator Concentations Versus F7 Parameter for Station P Winter Conditions

Ecosystem Stability. The question of ecosystem stability is a complex one that became an issue in evaluating some initial OPED/Optimization Model results for the 4-component ecosystem. These steady state solutions are not necessarily stable conditions that will endure even if the driving environmental forces remain constant. In fact an unstable solution was found for the summer conditions at Station P (see Section 4.2) for small allowable f7 values (i.e., 0.01 per day). This is illustrated by the simulatione in Figure 5. The OPED/Variational Model was used here assuming steady state parameters and constant environmental conditions but with small (1%) perturbulations in the initial concentration levels of each component. Severe oscillations begin after about 10 days and continue over the remainder of the simulation time period as substantial changes in component concentrations occur. Contrast this result with the simulation run in Figure 6 corresponding to a steady state solution where the minimum allowable f7 value was increased causing decreased predator levels. The latter ecosystem state appears quite stable; this was confirmed when perturbed component levels as high as 10 percent still gave a similar stable response.

One of the most significant results of the present ecosystem studies is that, in fact, the model response characteristics are quite stable for the parameter sets derived to represent the available data. This means that ecosystem dynamics are related to changes in the environmental drivers and not to frequency components inherent in the mathematics of the model. Such non-linear formulations are often prone to such behavior and do not reflect observations for most plankton ecosystems. Parameter estimation is a critical factor in eliminating artifical oscillatory responses from predictive behavior.

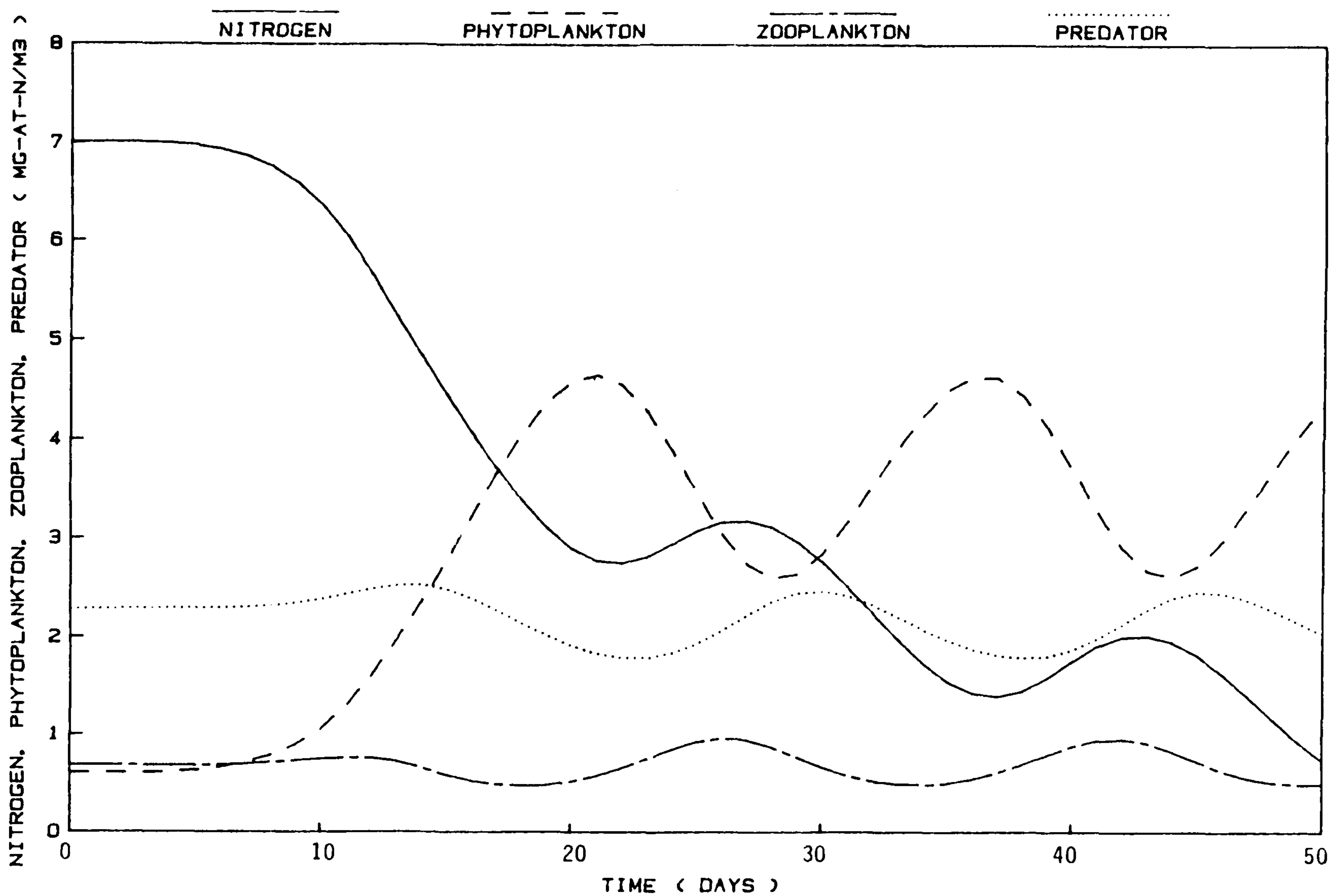


Figure 5. Unstable Steady State Solution for Summer/August Conditions at Station P

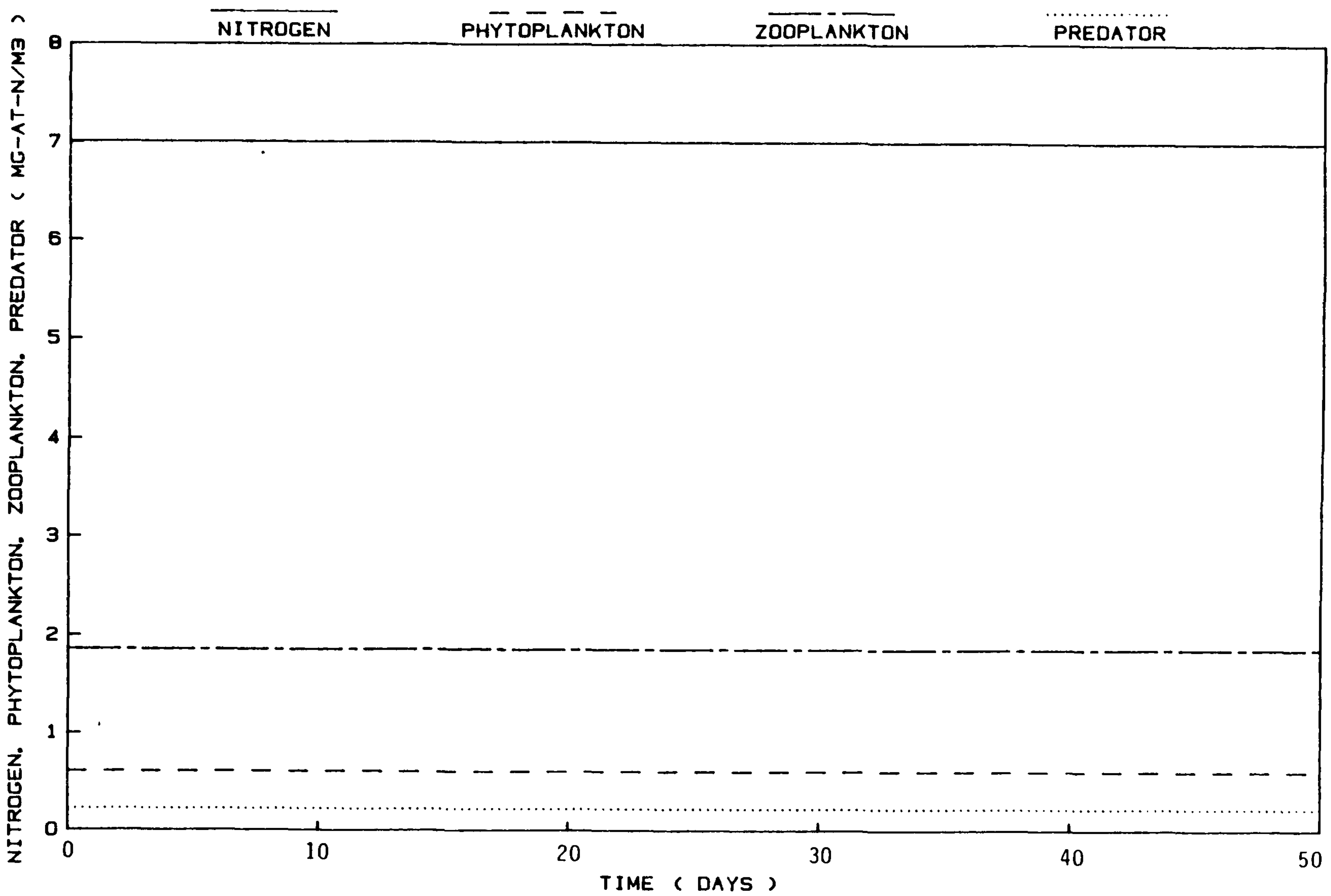


Figure 6. Stable Steady State Solution for Summer/August Conditions at Station P

4-Component versus 3-Component Ecosystem. The 4-component model implemented with the objective of defining a mechanism, i.e., visually oriented predators, that would drive distinctive vertical patterns of zooplankton reflecting observations. In fact, comparisons with the 3-component results for Station P did not show any distinct difference for the computed zooplankton distributions. Furthermore, the additional predator component introduces a whole new set of grazing and loss parameters that are ill-defined at best. Since the purpose of the modeling is to represent the biochemical distributions only to the extend that they can be correlated with and applied to describing optimal parameters, the simpler 3-component approach was deemed as most appropriate at the present time. Further evaluations of this selection will be made as the study proceeds and other ocean regions are analyzed.

4.2 Steady State Analysis of Ecosystem Variables

In determining OPED Model parameters to represent the Station P biochemical dynamics, two extreme seasonal conditions, January and August, were selected for the analysis. Persistent biochemical properties are assumed such that steady state mathematical formulas could be applied. This is a good approximation as reasonably constant winter and summer conditions are observed to exist for extended periods. Solving for two sets of parameters corresponding to winter and summer, the yearly cycle of ecosystem response can then be predicted as described in the following section.

The fixed and variable parameter values used for the OPED/Optimization Model analysis of winter and summer steady state conditions are presented in Table 1. A range of values is given for the variable parameters along with the optimal values computed by the OPED Model. The basis of this optimization is

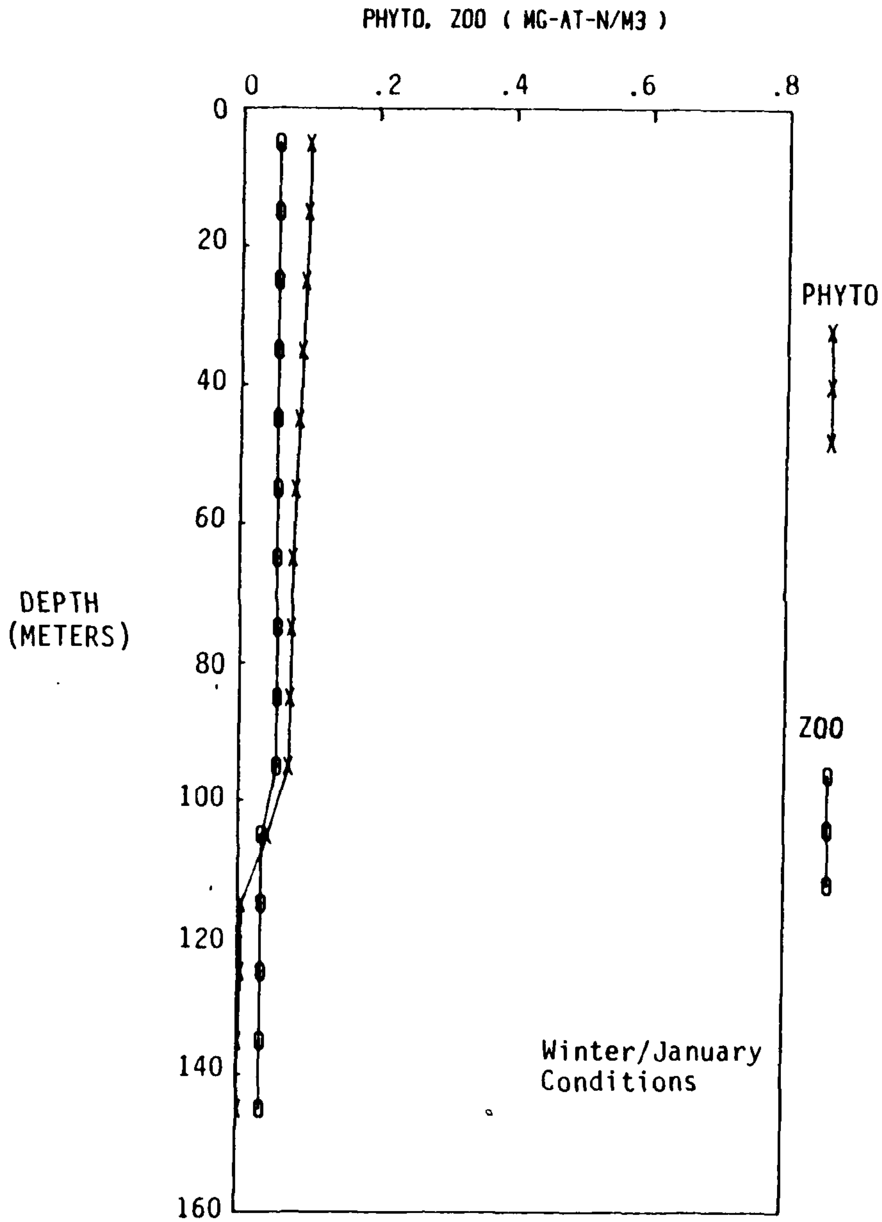
Table 1. Ecosystem Parameters in Steady State Analysis of Station P

Parameter	Description	Units	Fixed Constant or Variable Range/Optimum: Winter	Summer
Fixed:				
D_m	Mixed layer depth	meters	100	20
E_o	Surface irradiance	einsteins/m^2-day	5.0	25.0
T_s	Surface temperature	^oC	5.8	12.0
N_s	Surface Nitrogen	mg-at-N/m^3	15.	7.
N_B	Bottom Nitrogen (150m)	mg-at-N/m^3	30.	30.
P_s	Surface phytoplankton	mg-at-N/m^3	.1	.2
f_{1max}	Maximum photosynthetic rate	1/day	1.00	1.30
K_N	Nitrogen limiting half-saturation	mg-at-N/m^3	.1	.1
K_E	Light limiting half-saturation	einstein/m^2-day	2.	2.
m	Maximum nitrogen assimilation efficiency	mg-at-N/einstein	0.10	0.10
K	Scalar irradiance half-saturation	einstein/m^2-day	10.	10.
Variable:				
Z_i	Zooplankton in Layer i	mg-at-N/m^3	0-.25/see profile	0-.8/see profile
f_1	Nitrogen uptake in surface layer	1/day	.1-.6/.5526	.4-1.3/1.128
m	Maximum grazing	1/day	.1-2./2.0	.1-2/2.0
K_p	Grazing half-saturation	mg-at-N/m^3	.1-2./.2844	.1-2/.5410
f_2	Grazing in surface layer	1/day	.1-.4/.3073	.2-.4/.3405
f_4	Excretion plus predation	1/day	.05-.4/.09837	.05-.4/.1036

maximum solar energy utilization by the zooplankton throughout the water column as discussed in Section 4.1 and by Atkinson (1987a). Constraints include the variable ranges indicated in Table 1 plus the assumed steady state. Note that the zooplankton concentrations in each depth layer are treated as independent variables. The optimal distributions describe values in a number of vertical layers down to 150 meters: three 50-meter layers for the winter/August case and six 25-meter layers for the summer/August case.

The optimal zooplankton distributions for winter and summer are shown in Figure 7 along with the corresponding steady-state phytoplankton distributions. These plankton profiles should be compared with the deep 100-meter mixed layer that exists in January and the shallow 20-meter mixed layer in August. Note that the zooplankton generally track the phytoplankton concentrations, although there are additional zooplankton found at depths for the winter solution.

In Figure 8 corresponding to the January optimization case, the photosynthetic rate is shown to drop off by about 60 meters such that production is less than the assumed constant respiration rate of 0.1 per day, thereby defining the euphotic depth. Rapid mixing within the mixed layer allows for maintenance of the deeper phytoplankton stocks. The chlorophyll increases with depth down to 100 m although this assumes that the cells instantaneously adjust to local light levels instead of effectively integrating light levels during the short turnover times within the mixed layer. This modeling assumption may need to be modified in order to reflect the data for deep mixed layers. Diffuse attenuation k(PAR) tracks the chlorophyll levels as indicated in the figure and as described by Equation 15 in Section 3.2.



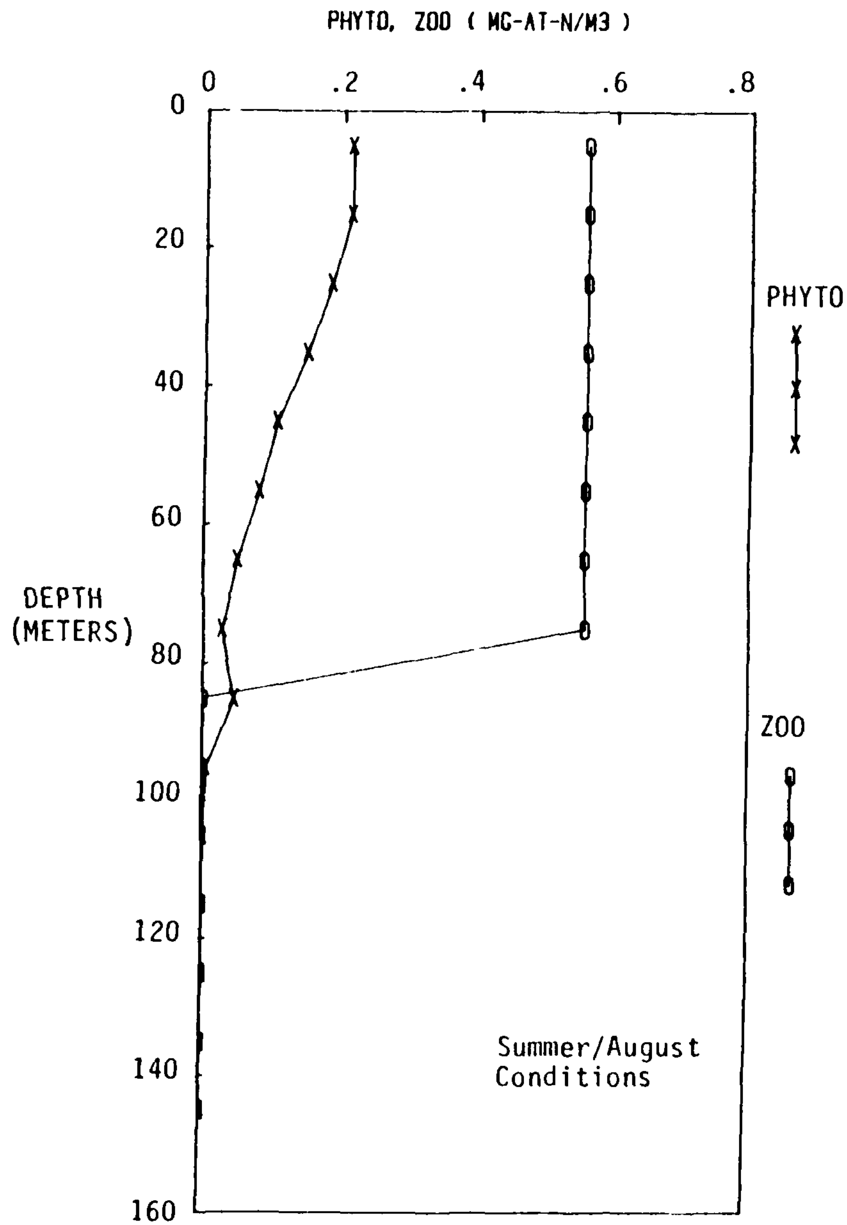


Figure 7. Optimal Zooplankton Distribution and Phytoplankton Profiles for Winter and Summer Conditions at Station P

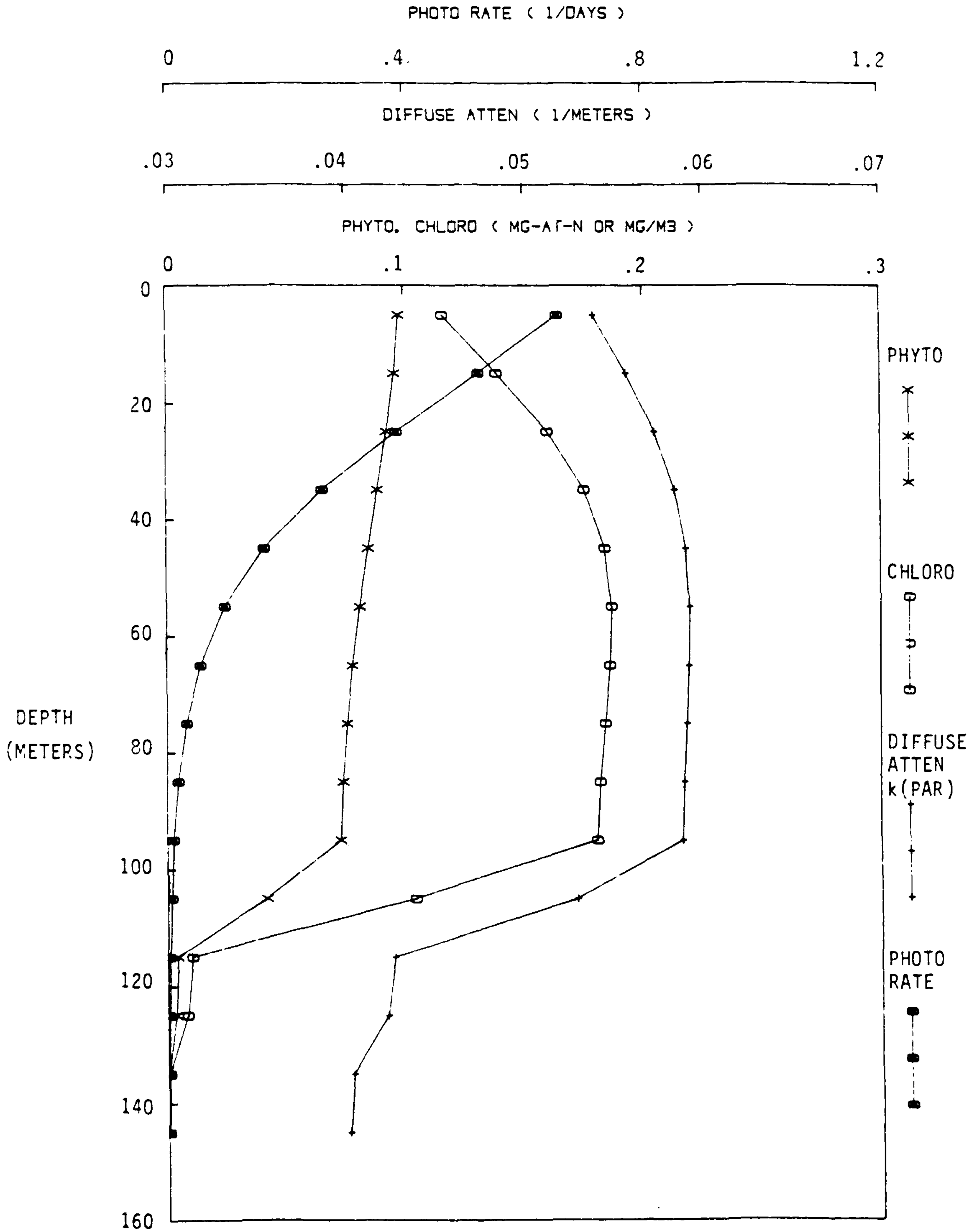


Figure 8. Steady State Profiles of Phytoplankton, Chlorophyll, Photosynthesis and Diffuse Attenuation for Winter Conditions at Station P

The summer/August conditions in Figure 9 are quite destinct from the winter/January conditions. Here the phytoplankton levels fall off gradually below the shallow mixed layer. Photosynthetic rate at the surface is more than 50 percent higher than the winter rate and maintains a euphotic depth down to about 80 meters. Also, subsurface peaks in chlorophyll and diffuse attenuation coefficients are predicted at about 40 meters.

One additional study using steady state assumptions was performed to establish the validity of the "light model", i.e., the phytoplankton-chlorophyll-diffuse attenuation relationships. A comprehensive data set taken at Station P in July 1986 (Anonymous) provided estimates of phytoplankton as derived from beam attenuation (c) measurements (Kiefer, 1988b) and profiles of chlorophyll and diffuse attenuation (k). The analysis consisted of using the OPED/Variational Model to match the phytoplankton and, hence, c distribution with depth and then comparing the resulting calculations of chlorophyll and k with measurements. Model parameters were set from the above analysis for summer conditions, except for the zooplankton concentration profile and two light model parameters. The zooplankton variables allowed for matching the phytoplankton profile while the light model parameters could then be adjusted to relate chlorophyll and diffuse attenuation to the phytoplankton. The two light model parameters, Φm and K_{ϕ}, are defined as maximum quantum efficiency for nitrogen assimilation and the half-saturation constant for scalar irradiance, respectively (refer to Equation 10 in Section 3.2).

The OPED Model calculations are presented and compared in Figure 10 with the July 1986 measurements at Station P. After parameter adjustments, the OPED light model predictions are seen to be in excellent agreement with measurements. It is therefore

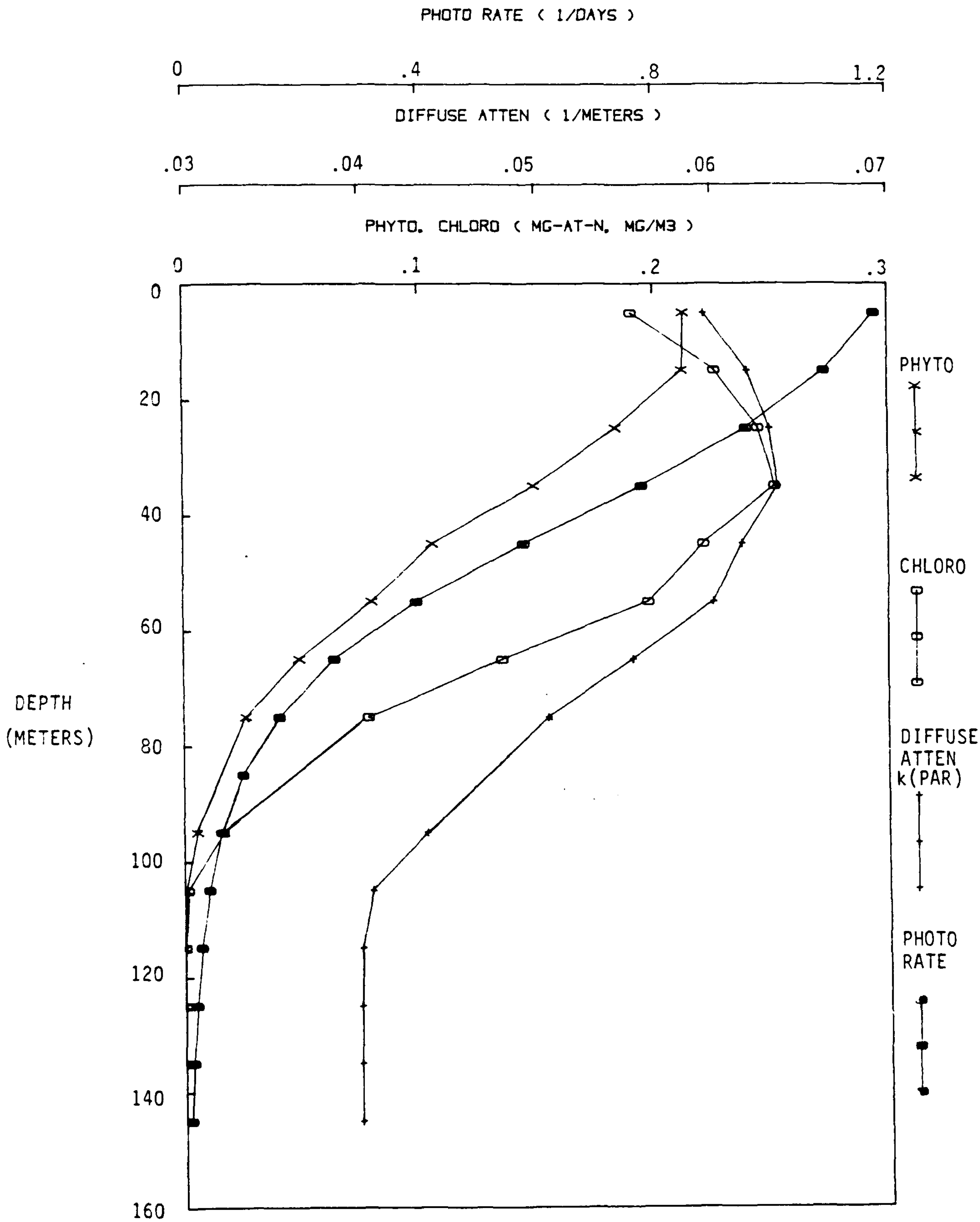


Figure 9. Steady State Profiles of Phytoplankton, Chlorophyll, Photosynthesis, and Diffuse Attenuation For Summer Conditions at Station P

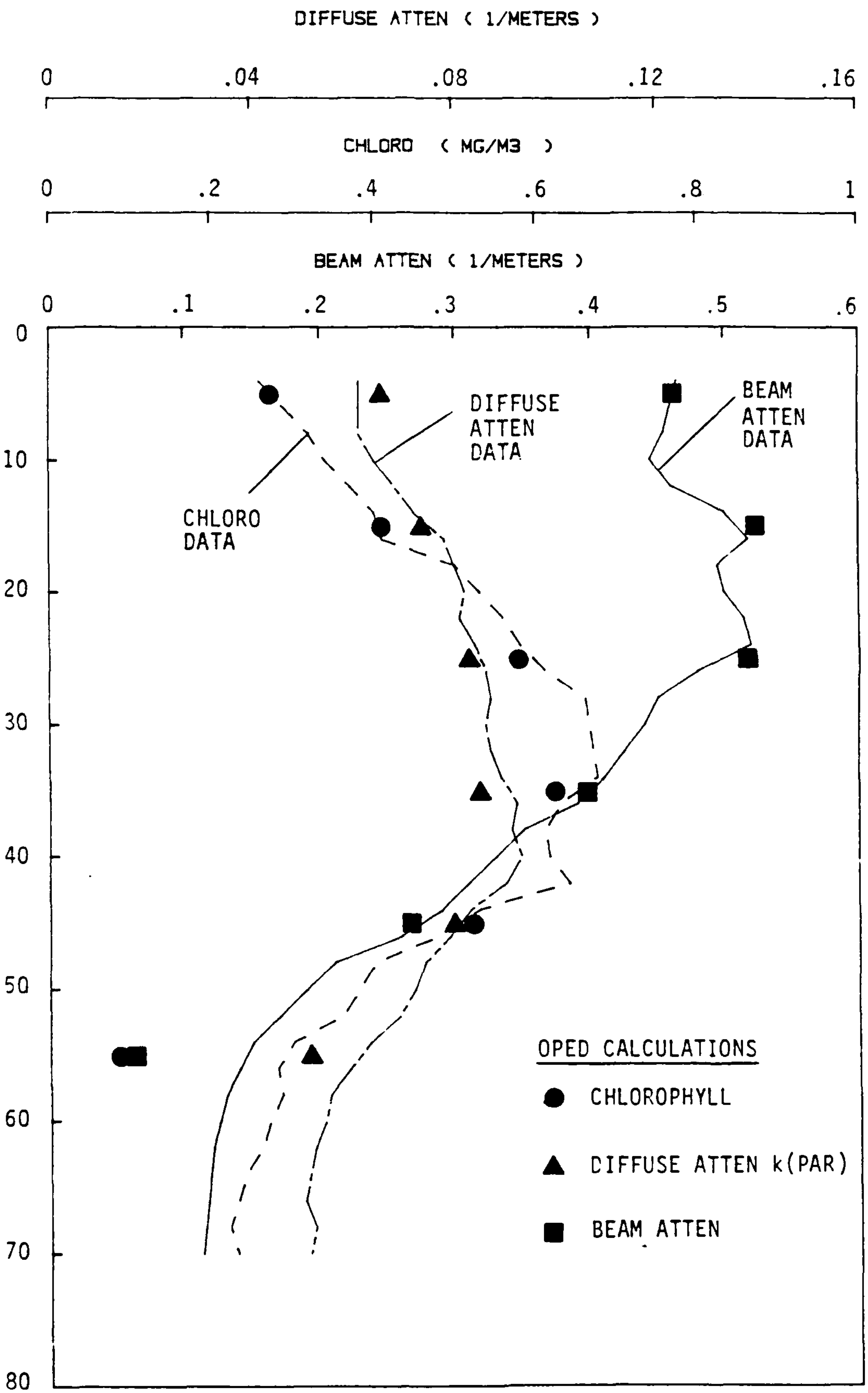


Figure 10. Comparison of Tuned OPED Light Model With Station P Measurements in July 1986 (Anon.)

judged to be an appropriate representation but one that needs further data sets to establish the appropriate parameter values for given ocean conditions. The universality of Φm and K_Φ in various ocean regions as previously assumed is an open question.

4.3 Prediction of Yearly Cycle

The above parameter sets for winter and summer conditions were used in the OPED/Variational Model along with the driving physical features of solar irradiance (Figure 2) and mixed layer depth/temperature structure (Figures 2 and 3) to compute yearly ecosystem response characteristics. Winter parameter variables were used for November through March corresponding to deep surface layers and low light levels, while summer variables were used for April through October when shallow layers and high light levels exist.

The predicted yearly variability in total phytoplankton and zooplankton within the water column is presented in Figure 11. Measured chlorophyll in the surface layer and net zooplankton are shown in Figure 12 for use in making comparisons, although these measurements are not directly related nor are the driving physical conditions the same as for the predictions. However, general agreement of the major features are most encouraging. The predicted phytoplankton and measured chlorophyll indicate rather small variations in stock sizes between winter and summer, while the zooplankton increase significantly between seasons. There are some differences in the exact time and extent of the summertime increases.

A series of predicted ecosystem features are described in Figures 14 through 16 by plots of time-depth isopleths; Figure 13 shows corresponding temperature isopleths derived from the data in Figure 3. In Figure 14 the phytoplankton levels vary somewhat

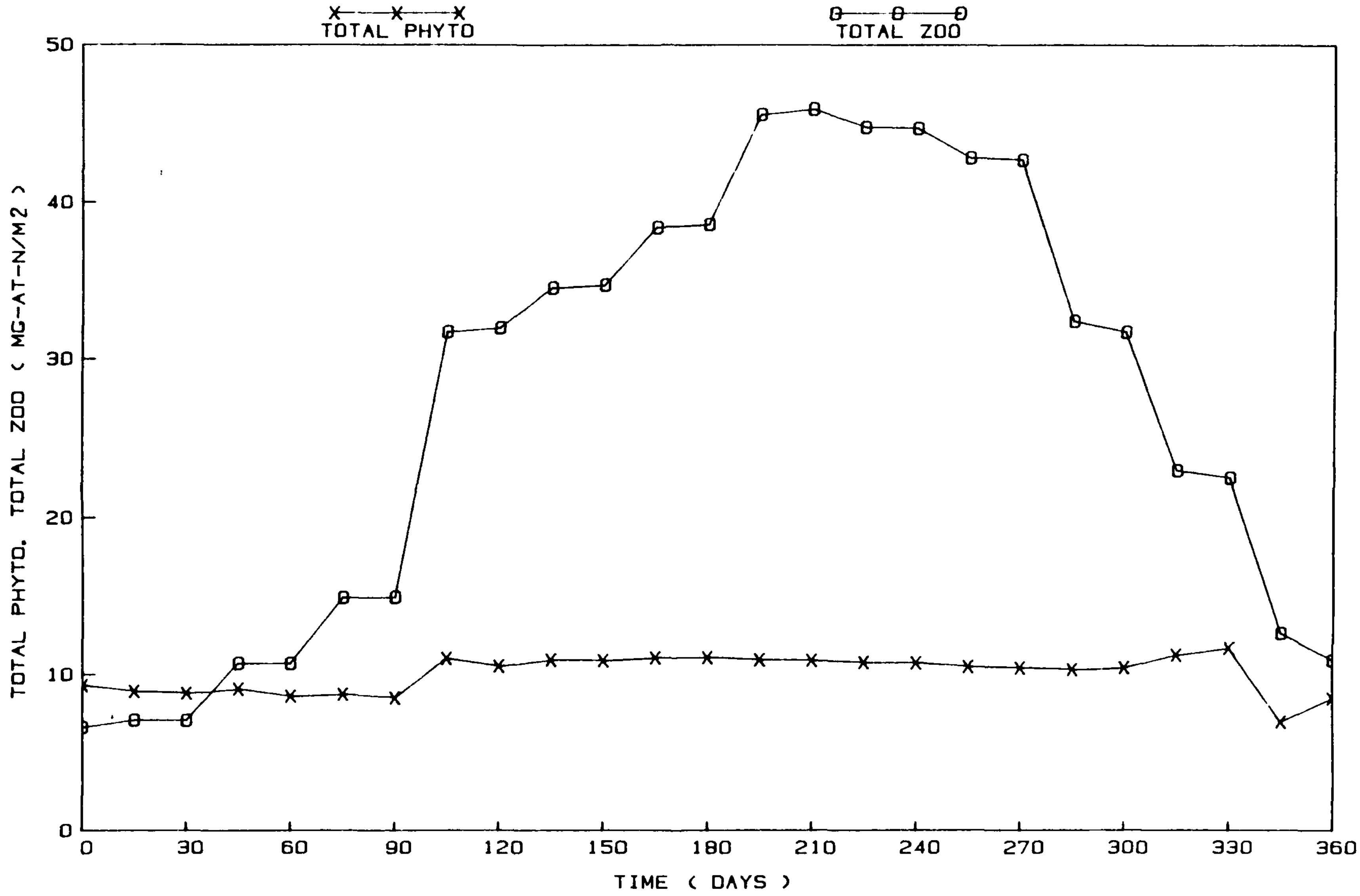


Figure 11. Predicted Yearly Variation of Total Phytoplankton and Zooplankton at Station P

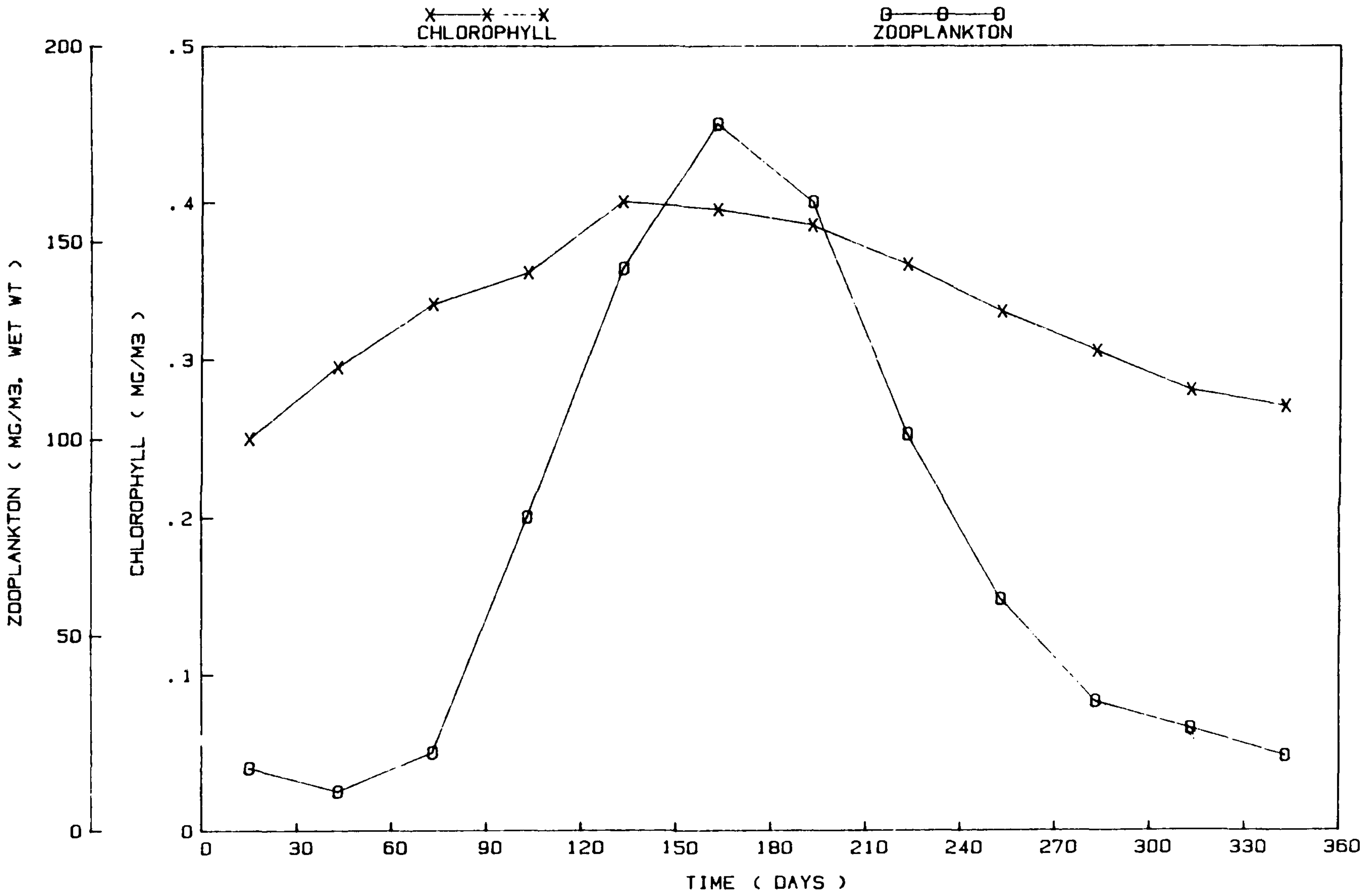


Figure 12. Mixed Layer Measurements of Chlorophyll and Zooplankton Wet Weight at Station P (Kiefer and Atkinson 1984)

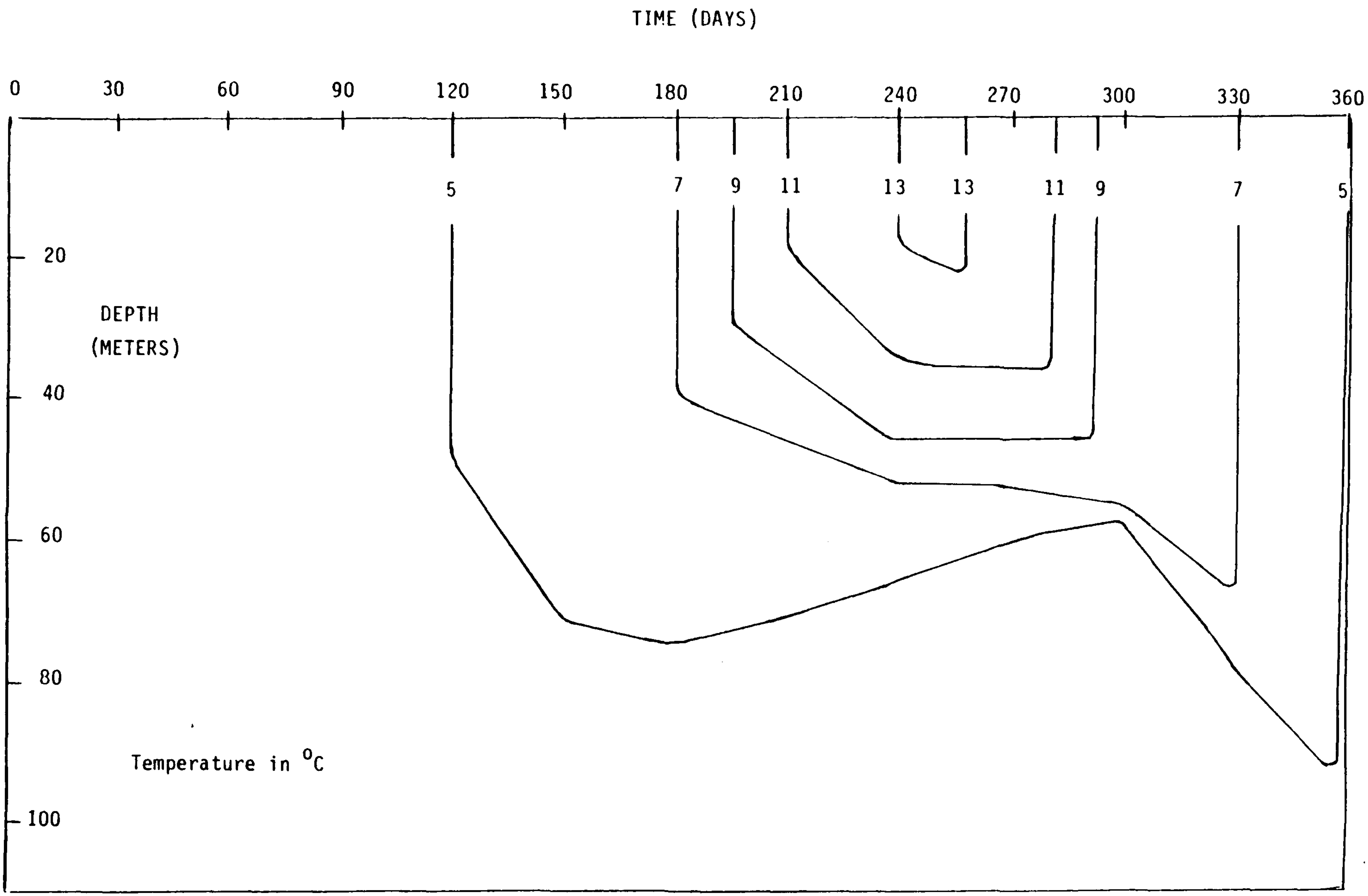


Figure 13. Temperature Time-Depth Isopleths at Station P

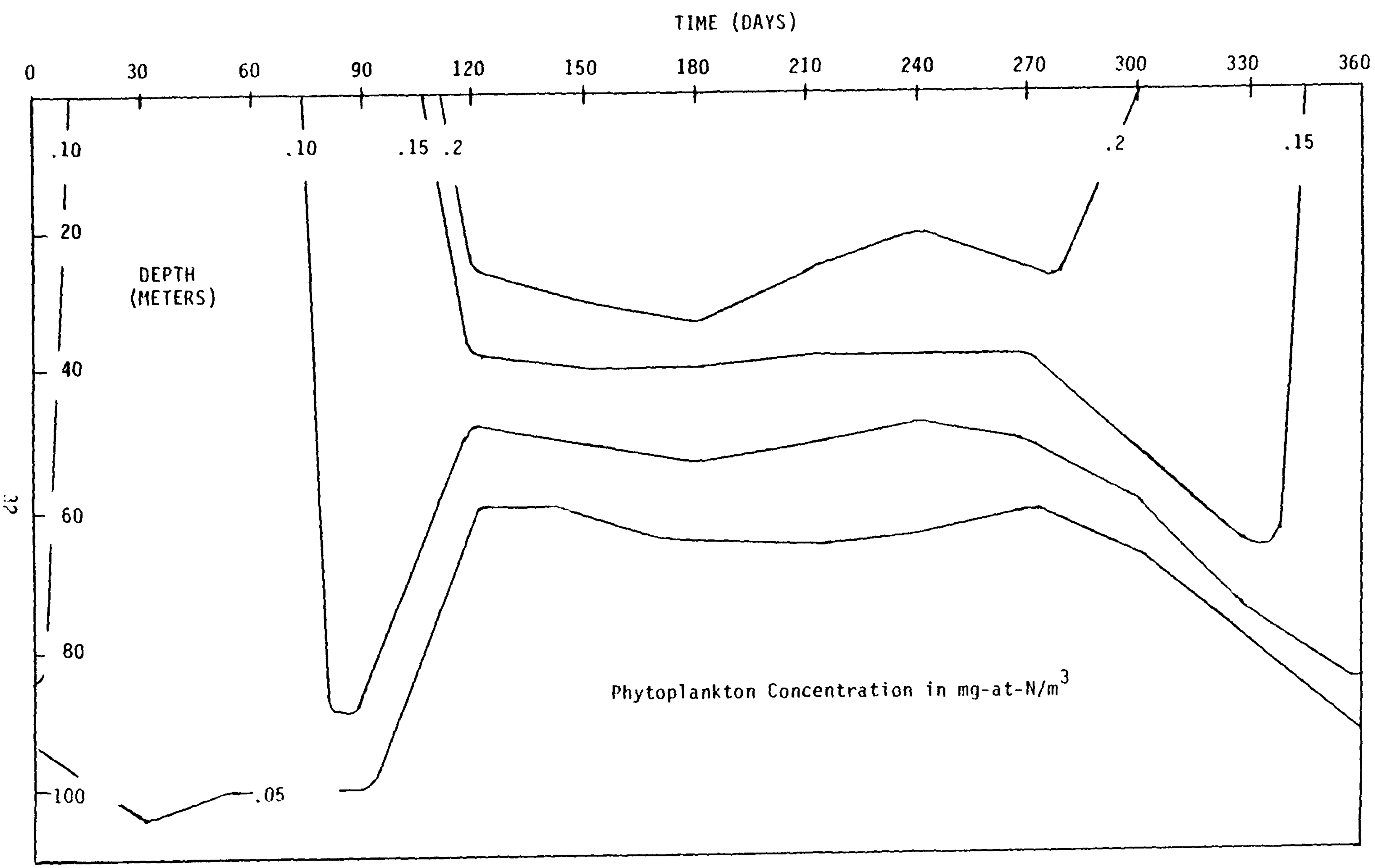


Figure 14. Phytoplankton Time-Depth Isopleths at Station P

symmetrically over the yearly time cycle, reaching summer levels at the surface about twice that in the winter. Zooplankton in Figure 15 increase to peak summer levels in August/September and at somewhat shallower depths then in the winter. Finally, Figure 16 describes the chlorophyll changes in time and depth. Here a later peak in October/November is observed at the surface, while a subsurface peak first appears in June/July. These features correspond to the combined effects of decreasing light levels with either depth or time causing increased chlorophyll per cell. This increase per cell can more than compensate for reduced cell concentrations.

It appears from initial comparisons of the predictions with the data sets that the OPED Model provides a reasonably good representation of the dynamic environment at Station P over the yearly cycle. Further data comparisons and model refinement would no doubt improve confidence in these preliminary results.

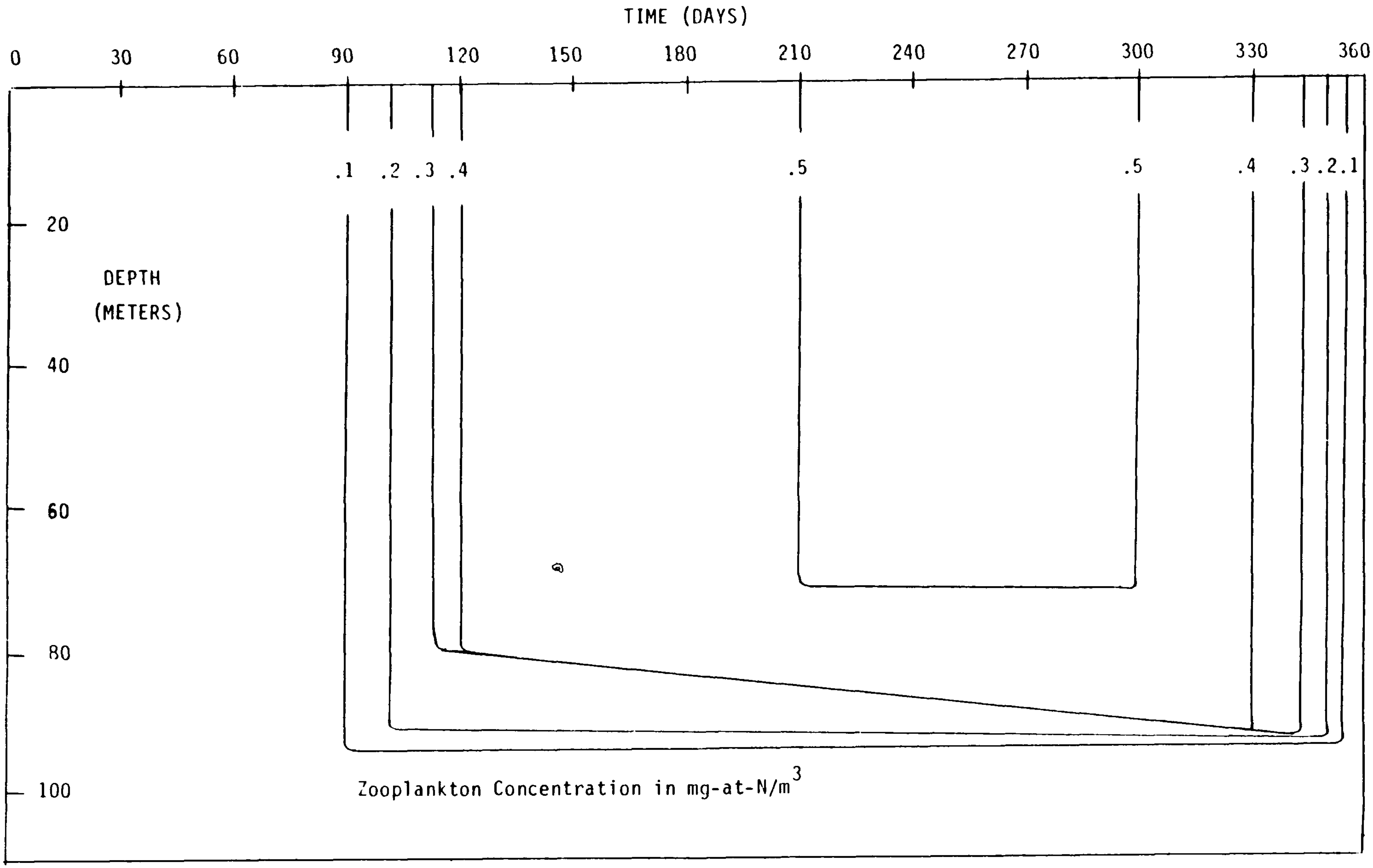


Figure 15. Zooplankton Time-Depth Isopleths at Station P

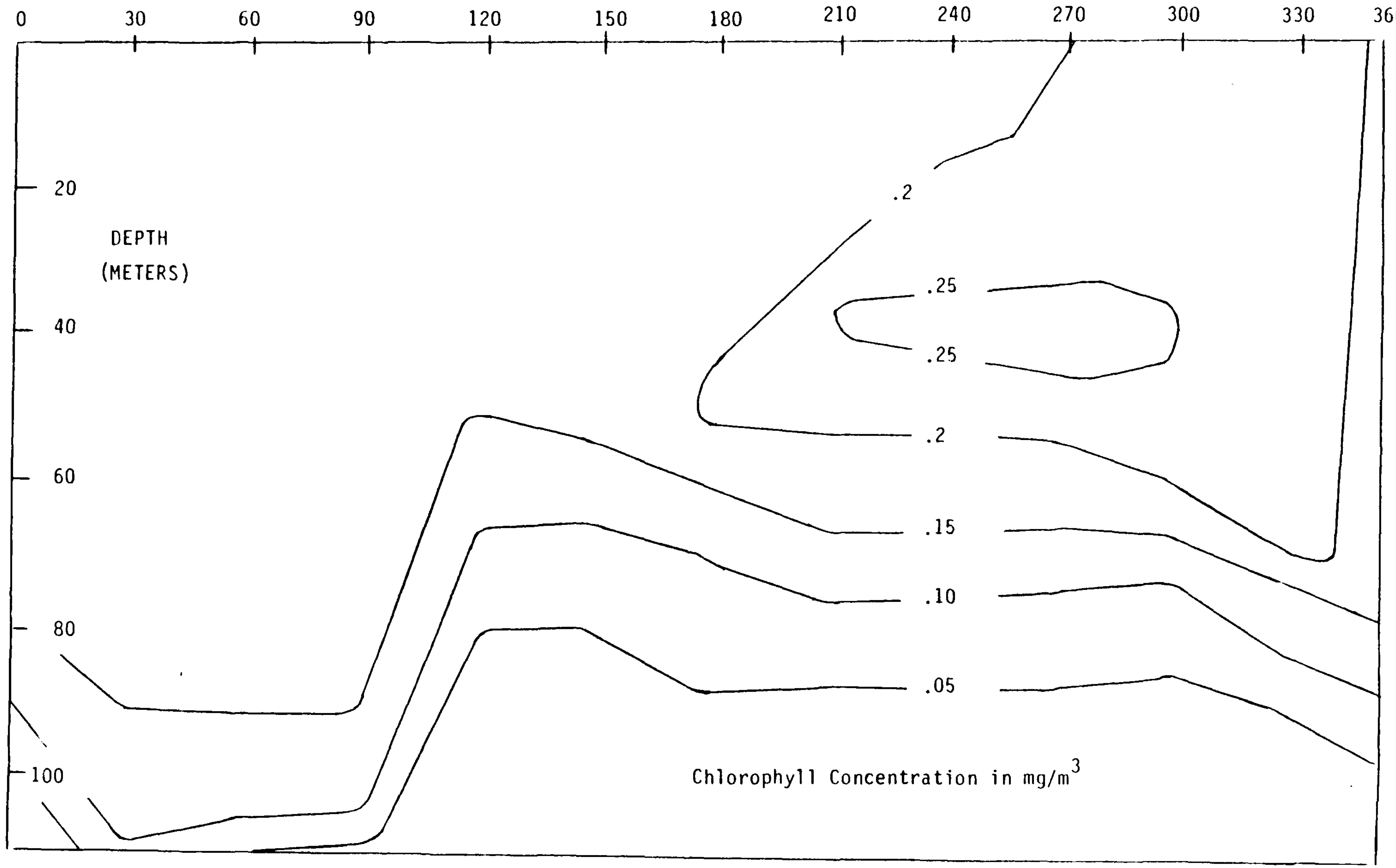


Figure 16. Chlorophyll Time-Depth Isopleths at Station P

5. OPED MODEL APPLICATIONS TO WEATHER STATION S ANALYSIS AND PREDICTION

The conditions at Weather Station S in the Sargasso Sea off Bermuda are in substantial contrast to those at Station P in the eastern North Pacific. The productivity of the ecosystem is limited, at least during the summer months, by the low surface nutrient concentrations. The water temperature and surface irradiance are both relatively high year round while the mixed layer can deepen from very shallow, 25 meters or so in the summer, to as much as 250 meters in the winter. The mixed layer depth and irradiance levels are plotted for a typical year in Figure 17 to illustrate the key forcing functions for this ecosystem.

5.1 Steady State Analysis of Ecosystem Variables

In the steady state analysis of Station S, March was selected as representative of winter conditions while September was selected for the summer season. The fixed and variable parameters corresponding to these two months are listed in Table 2 and were used as inputs to the OPED/Optimization Model tuning calculations.

The OPED solutions for optimal parameters are also listed in Table 2. The zooplankton distributions corresponding to the March and September solutions are shown in Figure 18 along with the steady state phytoplankton profiles. Parameter values are similar for both solutions except for nutrient half-saturation constant, K_N, and the optimal zooplankton profiles. Since the nutrient constant is only important for the summer conditions when low nutrient levels limit photosynthesis, the winter value is not relevant and therefore can be ignored.

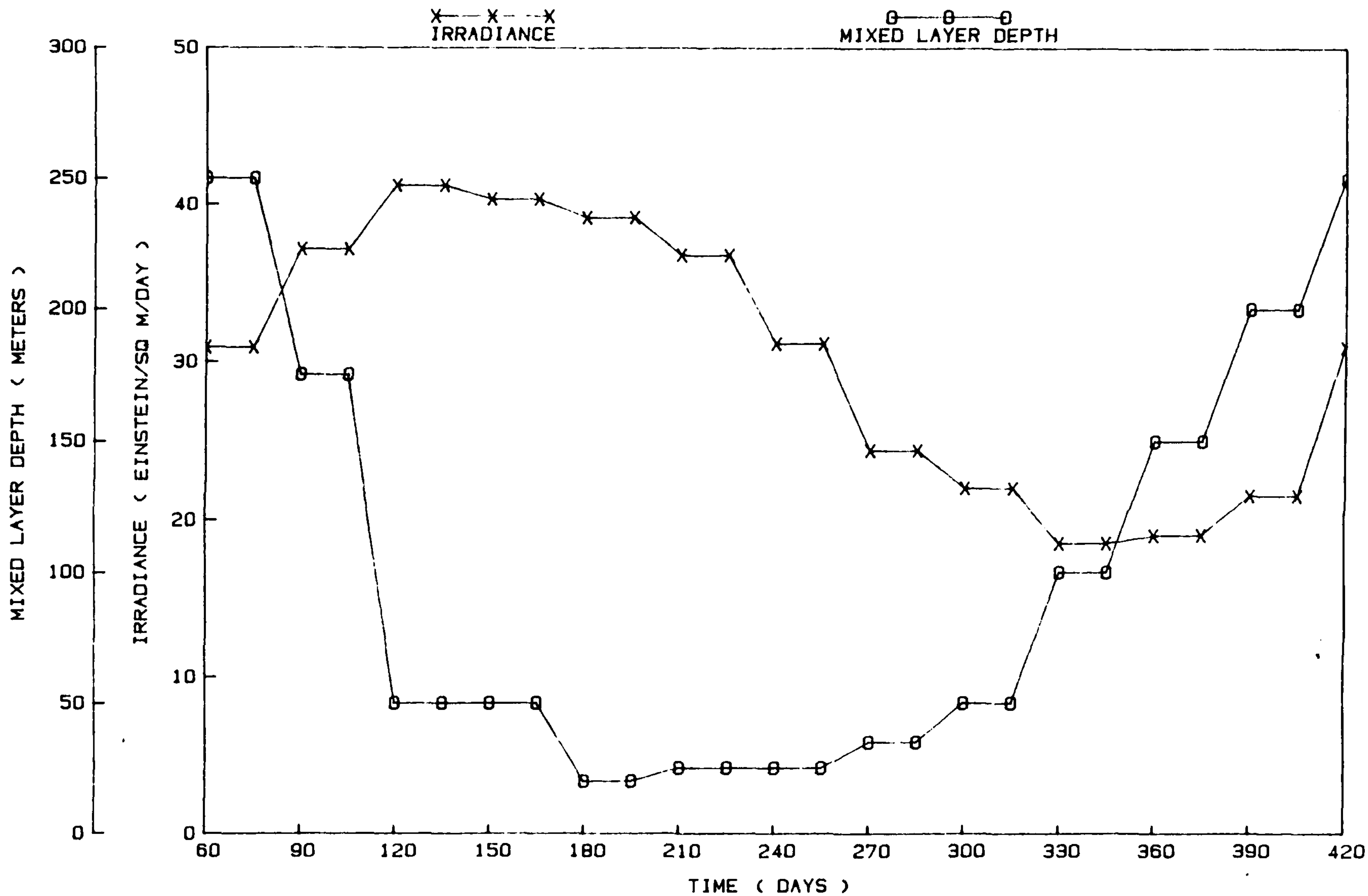


Figure 17. Variation of Surface Irradiance and Mixed Layer Depth Over Year At Station S

Table 2. Ecosystem Parameters in Steady State Analysis of Station S

Parameter	Description	Units	Fixed Constant or Variable Range/Optimal Winter	Summer
Fixed:				
D_m	Mixed layer depth	meters	250	25
E_o	Surface irradiance	einsteins/m^2-day	30.9	31.1
T_s	Surface temperature	^oC	19.1	27.0
N_s	Surface Nitrogen	mg-at-N/m^3	.7	.1
N_B	Bottom Nitrogen (300m)	mg-at-N/m^3	4.0	4.0
P_s	Surface phytoplankton	mg-at-N/m^3	.10	.08
f_{1max}	Maximum photosynthetic rate	1/day	1.60	1.76
ϕ_m	Maximum nitrogen assimilation efficiency	mg-at-N/einstein	.010	.010
K_ϕ	Scalar irradiance half-saturation	einstein/m^2-day	10.	10.
Variable:				
K_N	Nitrogen limiting half-saturation	mg at-N/m^3	.05-1./.100	.05-1./.351
K_E	Light limiting half-saturation	einstein/m^2-day	2-10/2.	2-10/2.
z_i	Zooplankton in layer i	mg-at-N/m^3	0-.8/see profile	0-.8/see profile
μ_m	Maximum grazing	1/day	.1-2./2.0	.1-2./2.0
K_P	Grazing half-saturation	mg-at-N/m^3	.05-2./.235	.05-2./.240
f_4	Execretion plus predation	1/day	.05-1./.1015	.05-1./.1003

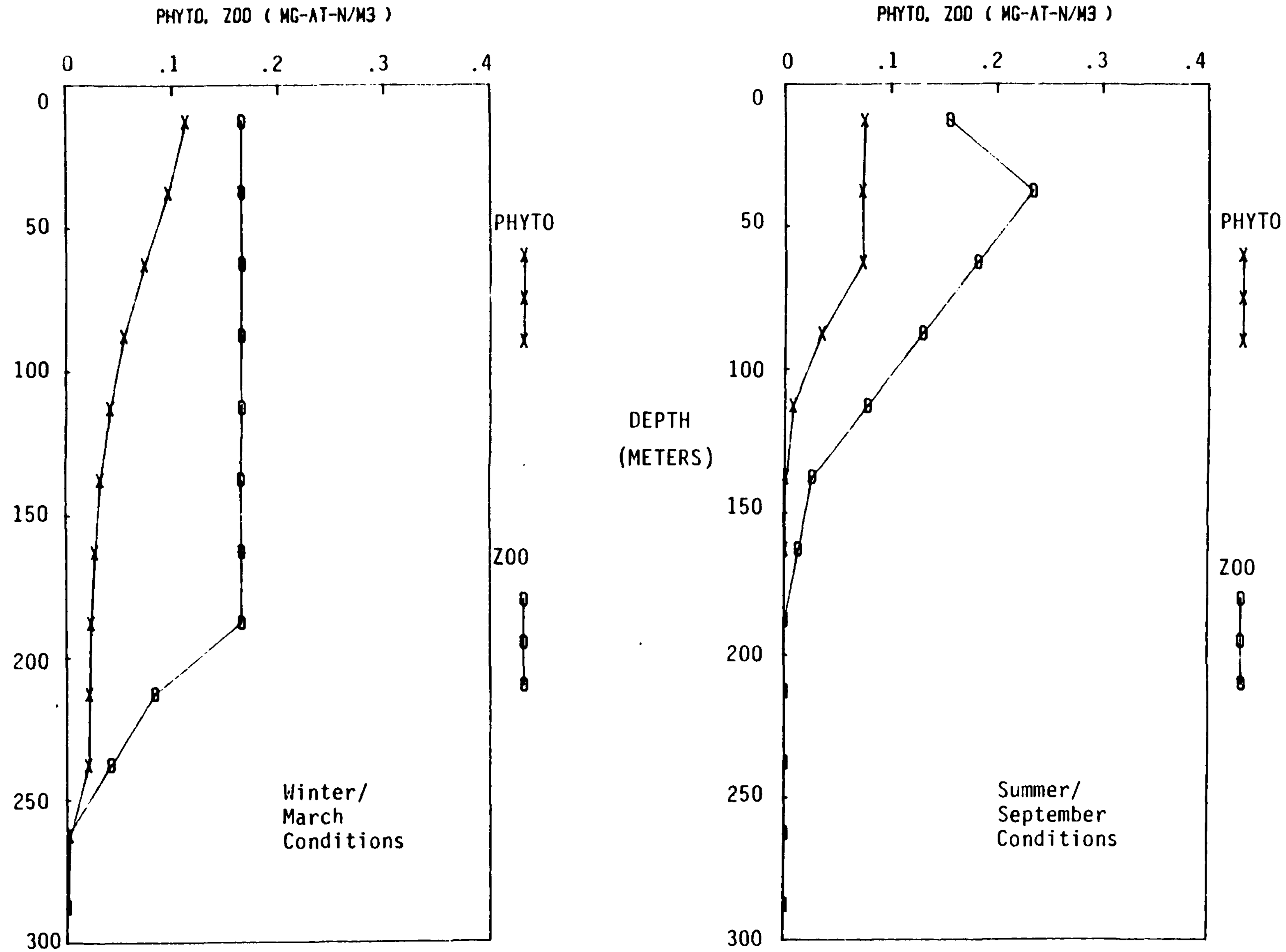


Figure 18. Optimal Zooplankton Distribution and Phytoplankton Profile For Winter and Summer Conditions at Station S

The zooplankton profiles in Figure 18 are quite distinct and reflect both the depth of the mixed layer and the concentrations of phytoplankton on which they feed. The winter zooplankton concentration remains constant down to near the bottom of the deep mixed layer at about 200 meters and then falls off to zero in the deep waters below 250 meters. In the summer, low nutrient levels limit production in the shallow 25 meter surface layer and a subsurface zooplankton peak is observed that takes advantage of the increased production just below the surface (see below). Zooplankton concentrations fall off to near-zero by 150 meters or so.

Predicted profiles of chlorophyll, diffuse attenuation, and photosynthetic rate along with phytoplankton are presented in Figures 19 and 20 corresponding to winter/March and summer/September optimal solutions, respectively. The winter production is seen to be quite large near the surface as nutrients are relatively abundant and light levels are reasonably high. On the other hand, the summer productivity at the surface is less than that in the immediate layers below the 25-meter mixed layer. The latter have higher nutrients than at the surface and still sufficient light for effective production. Rather strong subsurface chlorophyll and corresponding diffuse attenuation peaks result because of the persistence of phytoplankton concentrations below the mixed layer with photo-adaptation resulting in increased chlorophyll per cell.

5.2 Prediction of Yearly Cycle

The variations of phytoplankton and zooplankton within the water column are predicted in Figure 21 using the OPED/Variational Model and the parameters defined from the above steady state analysis.

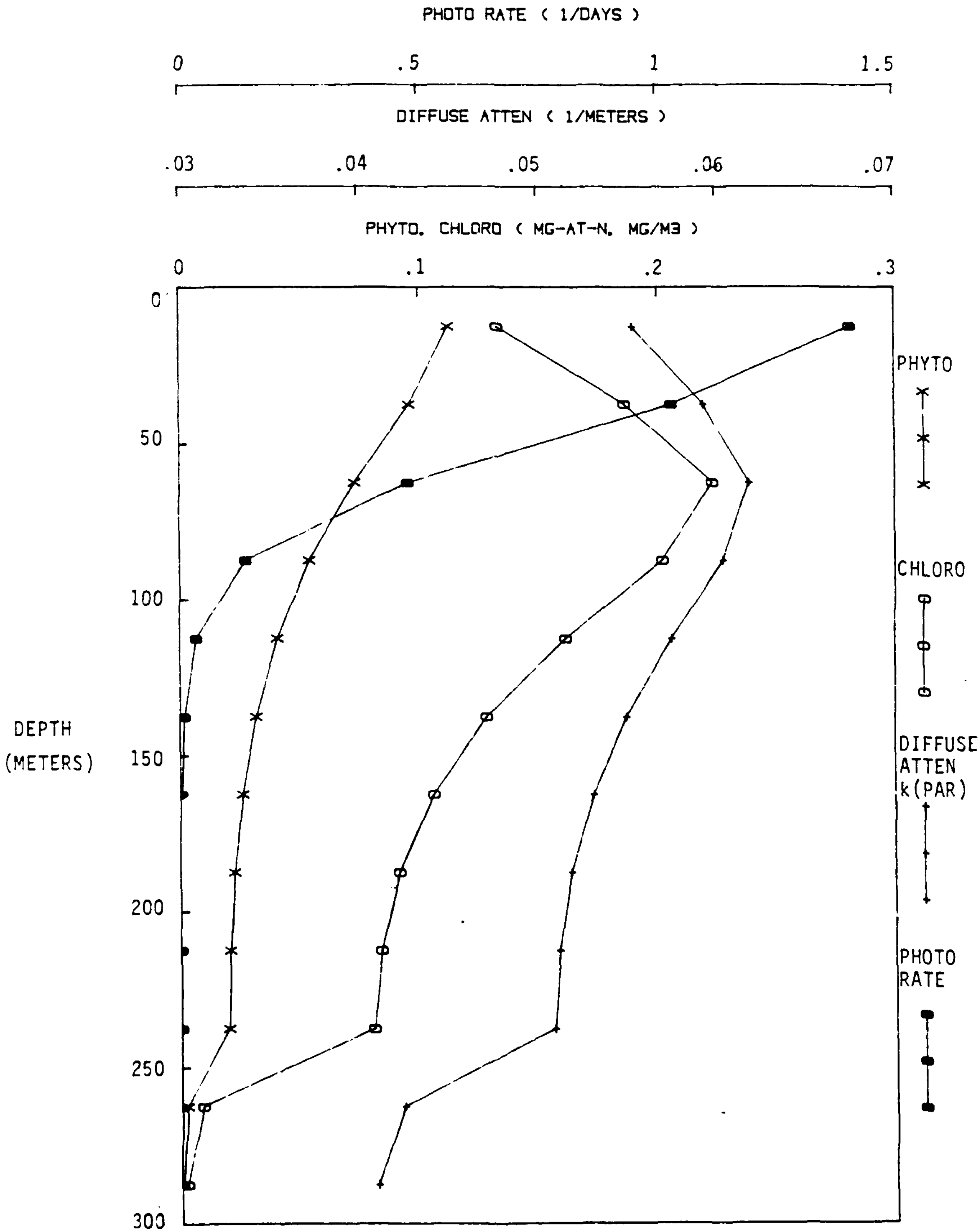


Figure 19. Steady State Profiles of Phytoplankton, Chlorophyll, Photosynthesis, and Diffuse Attenuation For Winter Conditions at Station S

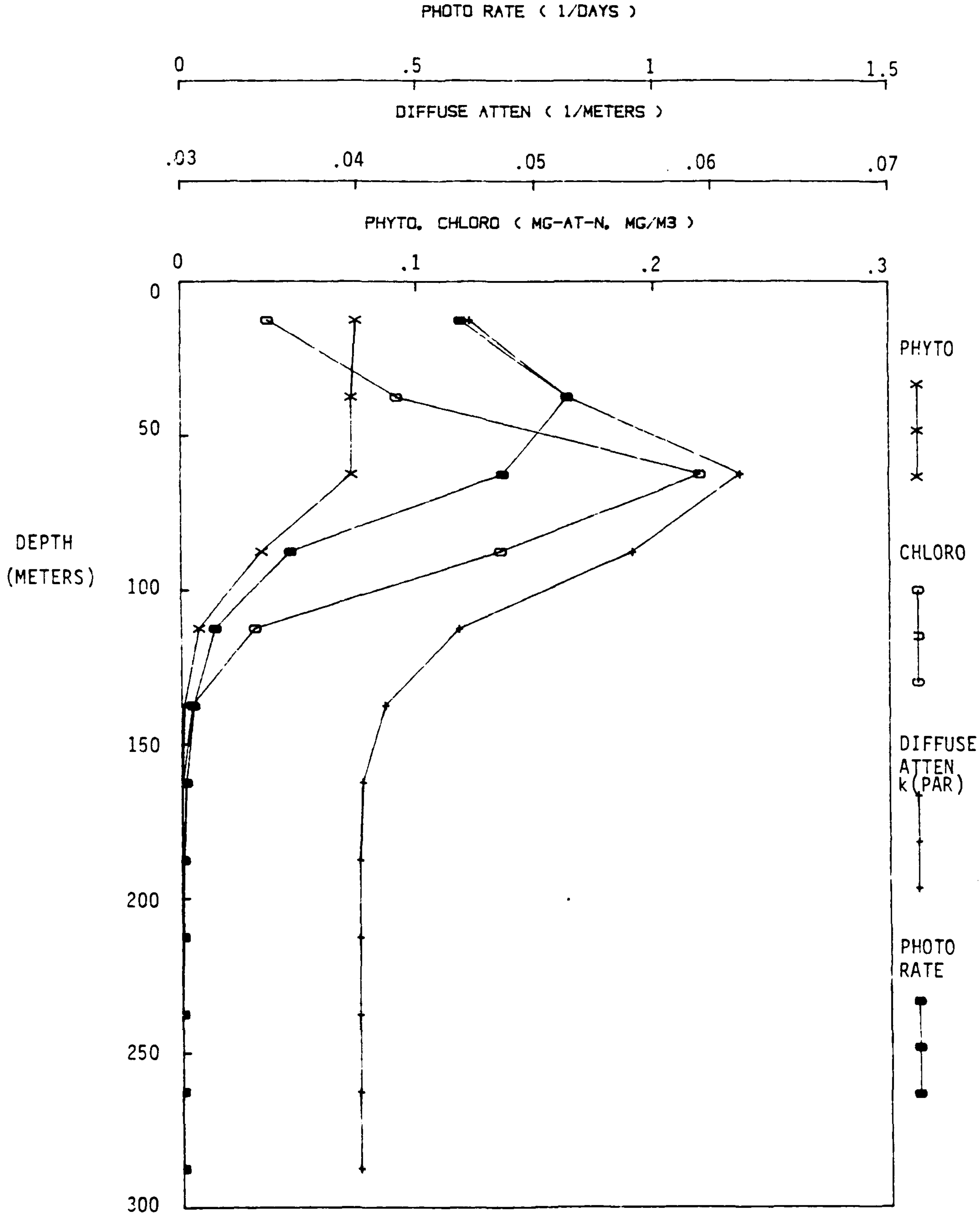


Figure 20. Steady State Profiles of Phytoplankton, Chlorophyll, Photosynthesis, and Diffuse Attenuation For Summer Conditions at Station S

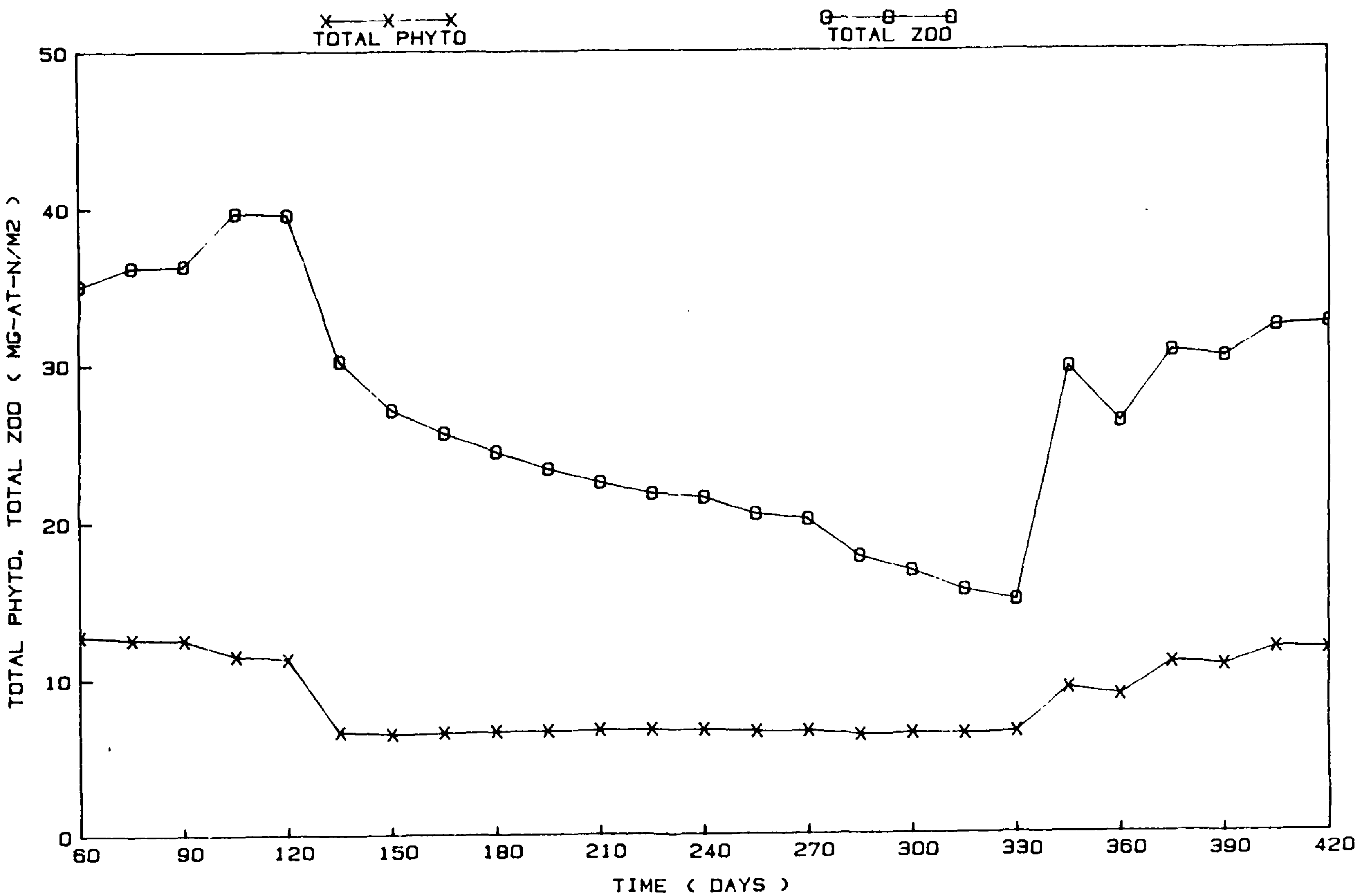


Figure 21. Predicted Yearly Variation of Total Phytoplankton and Zooplankton at Station S

The steady state winter solution was assumed to apply for December-April while summer solutions applied for May-November. The only significant difference between these solutions is the zooplankton distributions (see Figure 18).

The predicted plankton response in Figure 21 shows a winter maximum followed by decreases in both phytoplankton and zooplankton during the summer months. The phytoplankton decreases about 50 percent while the zooplankton stock is reduced somewhat more. The plankton levels then increase rather abruptly in the late autumn as deep mixing occurs (Figure 17) bringing nutrients to the upper water column for phytoplankton production.

Variations in the surface water (0-25 meters) concentrations are presented in Figure 22. The data indicate the large changes in surface nitrogen that occur during the year while phytoplankton and zooplantkon change less dramatically. Zooplankton within the second layer (25-50 meters) is also shown in Figure 22 in order to illustrate the predicted peak that occurs at this depth layer versus the upper layer.

Predicted time-depth isopleths showing the variations in temperature are given in Figure 23, while variations in beam attenuation and diffuse attenuation are provided in Figures 24 and 25, respectively. The attenuation isopleths at Station S are seen to reflect the temperature changes between winter and summer seasons as the shallow mixed layer is formed. The water in the summer is somewhat clearer at the surface and significantly clearer at depth since there is minimal deep mixing of the phytoplankton. Compare these figures with the profiles in Figures 19 and 20.

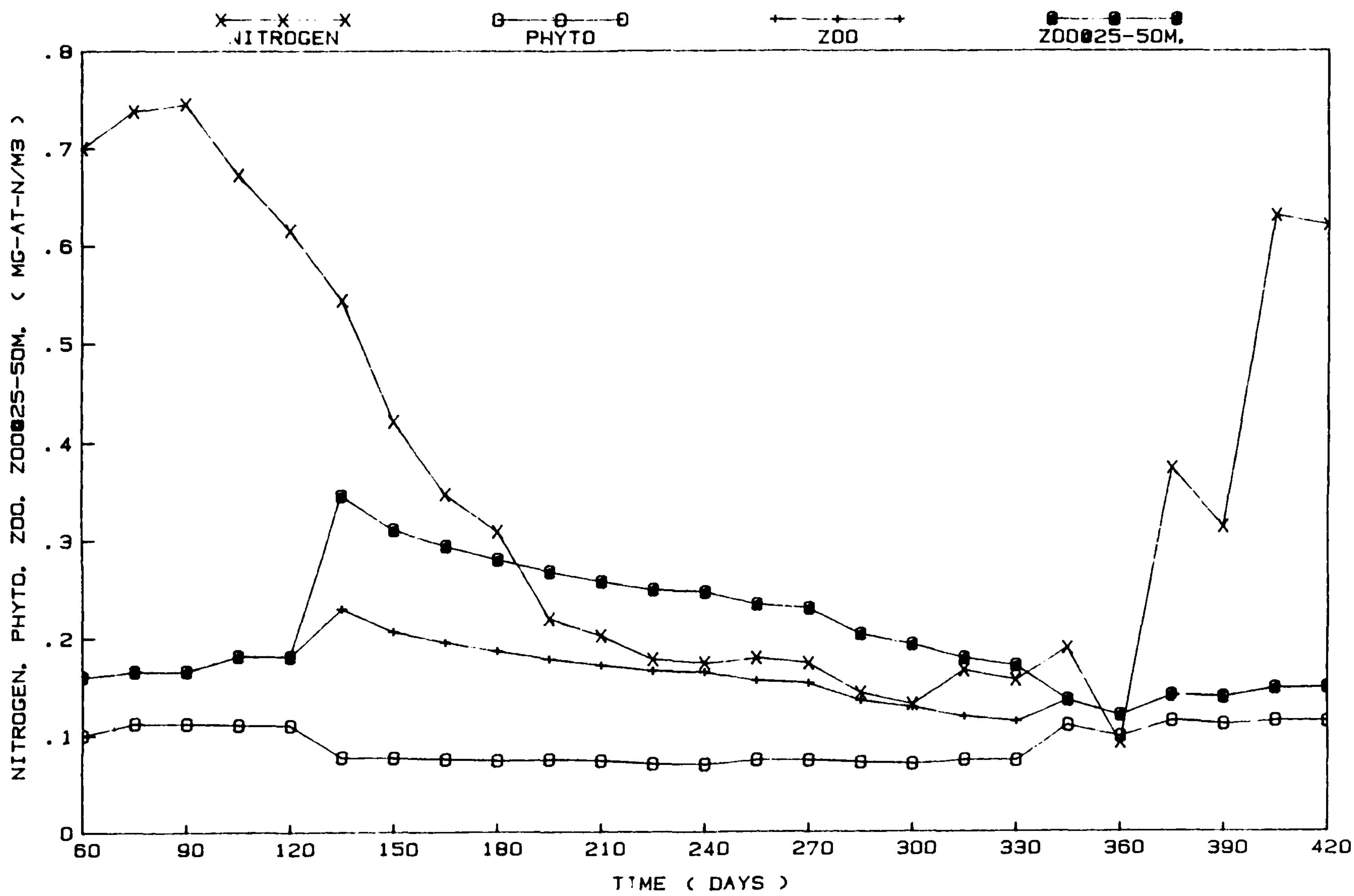


Figure 22. Yearly Variations of Surface (0-25m) Concentrations of Nitrogen, Phytoplankton, and Zooplankton and Deeper (25-50m) Peak Concentraions of Zooplankton at Station S

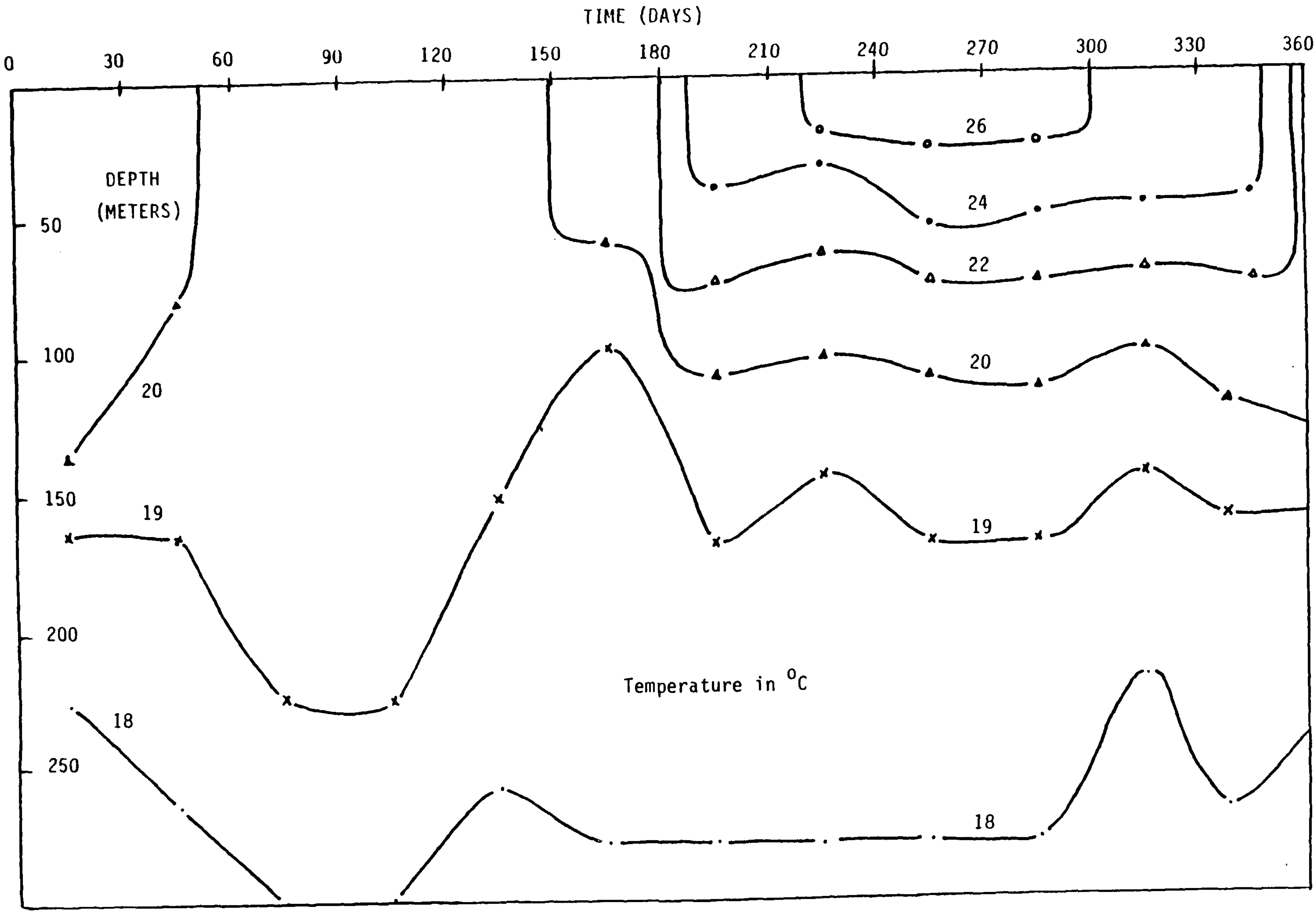


Figure 23. Temperature Time-Depth Isopleths at Station S

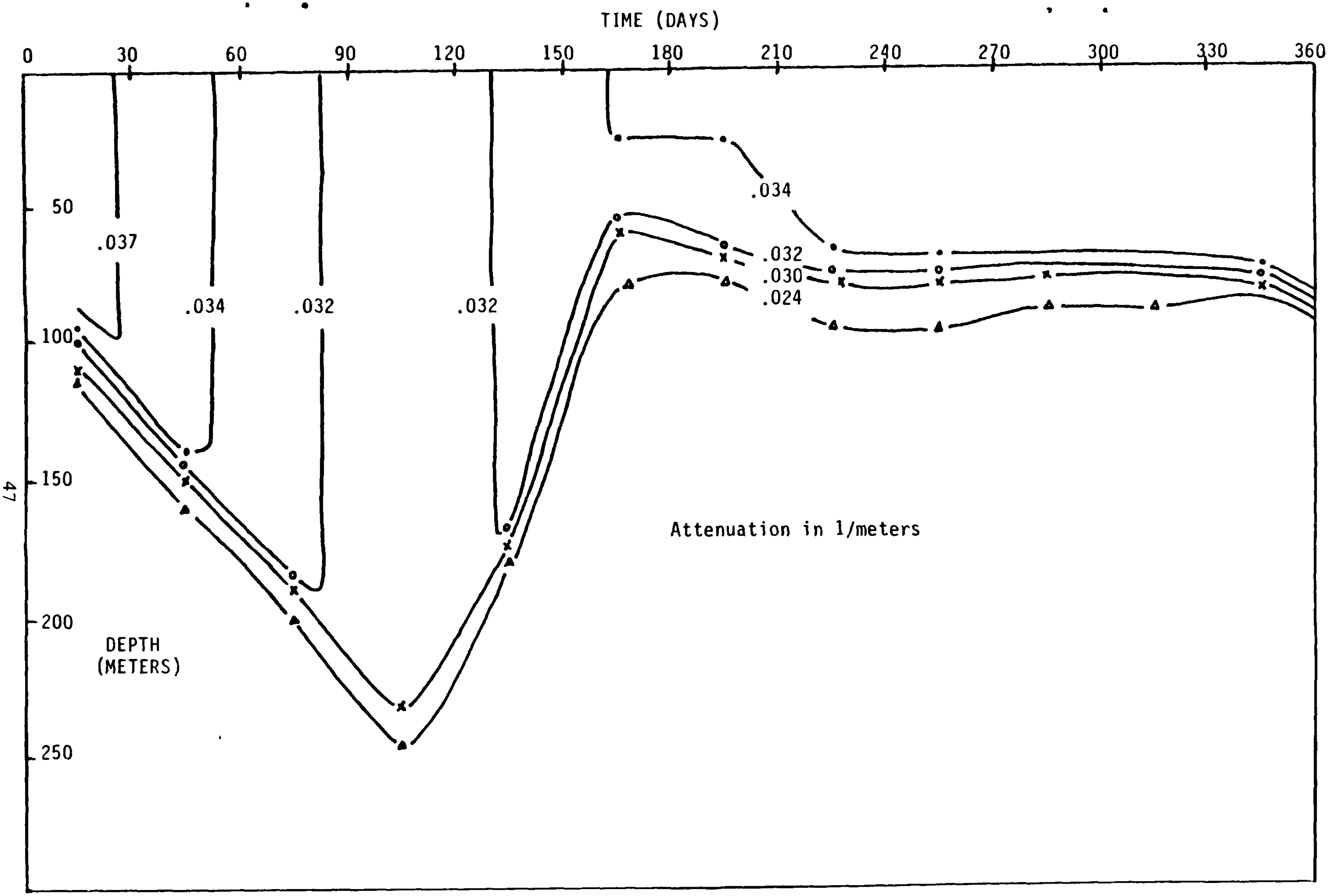


Figure 24. Beam Attenuation C(490) Time-Depth
Isopleths at Station S

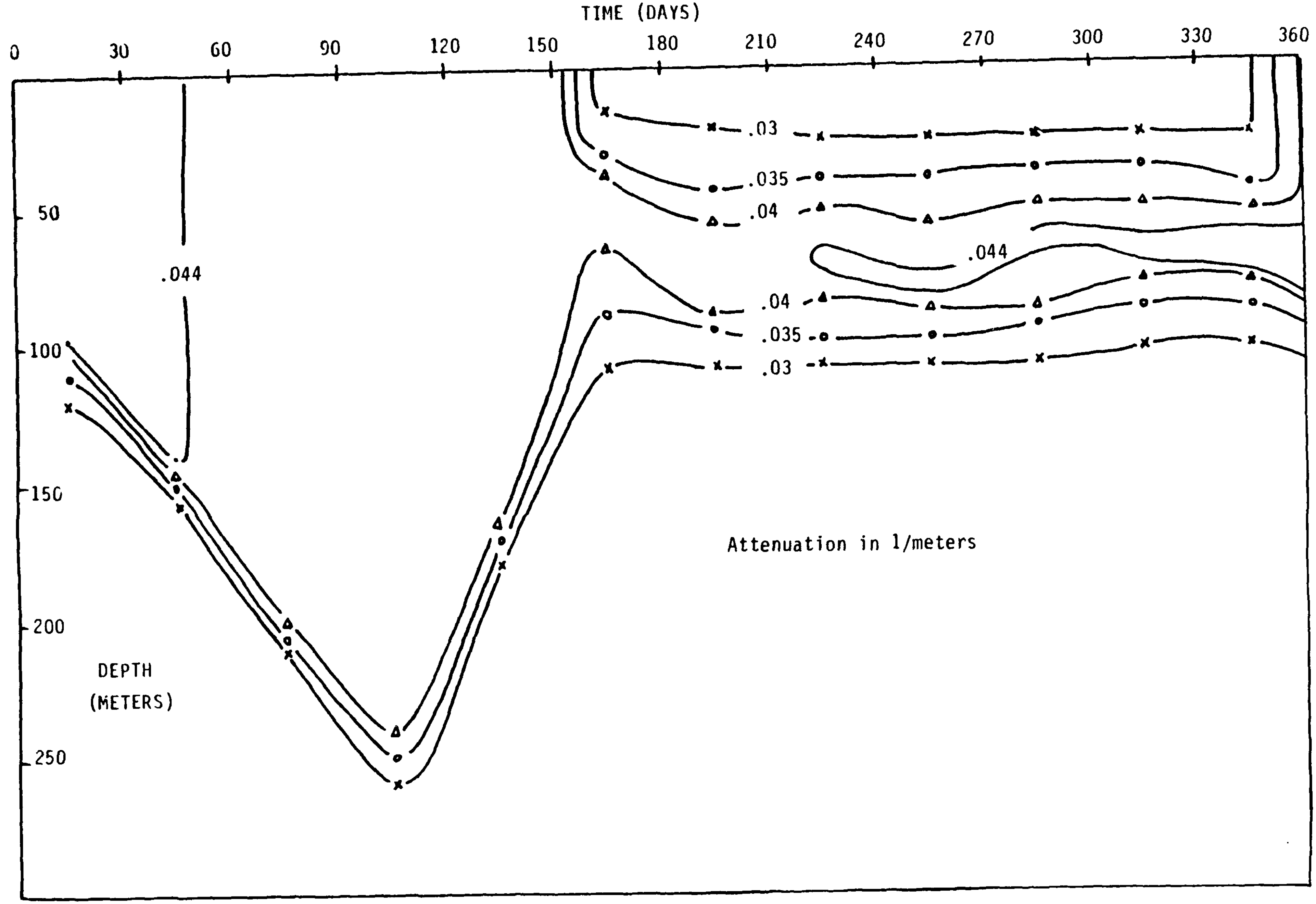


Figure 25. Diffuse Attenuation K(490) Time-Depth
Isopleths at Station S

6. CONCLUSIONS AND RECOMMENDATIONS

The OPED Model has been expanded to accommodate a predator component and to incorporate improved numerical procedures. The updated model has been used to analyze planktonic ecosystems at Weather Stations P and S and to tune model parameters for use in predicting response characteristics. Predictions were made describing both depth and time variations of the relevant ecological features over yearly cycles. The limited data agrees well with these predictions and gives confidence in the OPED Model applications to other ocean regions.

The objective of future applications will be to extrapolate in depth and in time from satellite imagery describing surface conditions. In particular, ocean-wide mappings of optical parameter profiles are to be generated. It is proposed that the OPED Model, in conjunction with supporting physical data, be used for these extrapolations.

Recommendations for achieving the above objective are to:

- analyze data from additional ocean regions and tune/modify the OPED Model to simulate observed conditions

- perform series of tests to validate and demonstrate the capability to predict optical profiles from satellite surface measurements.

- establish operational concept/procedure for providing routine estimates of optical properties within the water column to the Navy and other potential user groups

The promising results of the present study indicates that the program objective can be achieved if the work is continued.

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